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A Method for Finding the Limits of Application of the von Bertalanffy Growth Model and Statistical Estimates of the Parameters

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BAYLEY, P. B. 1977. A method for finding the limits of application of the von Bertalanffy growth model and statistical estimates of the parameters. J. Fish. Res. Board Can. 34: 1079–1084.

The following expression is derived expressing the instantaneous growth rate (G) in terms of length (l) the power of the weight–length relationship (b), and the Bertalanffy growth parameters (K and $L\infty$): $G = bK(L\infty/l - 1)$. Since this is valid for a length (or age) range in which growth conforms to the Bertalanffy model, a plot of G vs. $1/l$ should be linear with the intercept on the G axis being $-bK$ and on the $1/l$ axis being $1/L\infty$. Since the variables can be measured independently, deviations of points from the regression can be tested and the limits of validity of the model ascertained. In addition, confidence limits of K and $L\infty$ can be estimated. Two examples compare results with those using previous methods.

Key words: method, Bertalanffy, growth, statistical, estimates, parameters

BAYLEY, P. B. 1977. A method for finding the limits of application of the von Bertalanffy growth model and statistical estimates of the parameters. J. Fish. Res. Board Can. 34: 1079–1084.

L'équation suivante exprime le coefficient instantané de croissance (G) en termes de la longueur (l), de la puissance de la relation poids–longueur (b) et des paramètres de croissance de Bertalanffy (K et $L\infty$): $G = bK(L\infty/l - 1)$. Comme ceci est valide pour une gamme de longueurs (ou d'âges) dans laquelle la croissance s'accorde avec le modèle Bertalanffy, si l'on porte sur graphique G contre $1/l$, on devrait obtenir une droite dont l'intersection avec l'axe des G est de $-bK$ et avec l'axe $1/l$ de $1/L\infty$. Comme les variables peuvent être mesurées indépendamment, on peut vérifier la déviation des points à partir de la régression et s'assurer des limites de validités du modèle. En outre, on peut estimer les limites de confiance de K et de $L\infty$. Deux exemples permettent de comparer les résultats avec ceux obtenus à l'aide de méthodes antérieures.

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THE most common methods for assessing the applicability of the Bertalanffy model (von Bertalanffy 1934, 1938) and its parameters are those of Walford (1946), developed from Ford (1933), and the modification by Gulland (1964). Their main drawback is the lack of independence between the variables plotted. Also, departure from the model is not always clear graphically and cannot be tested statistically.

Another method by Beverton (1954, p. 57) requires trial values of the asymptotic length $L\infty$. This iterative method is complicated by the choice of age range over which the model is assumed to be applicable. A further problem is outlined below in Example 1.

Computer programs are available (Abramson 1971; Allen 1966, 1967) for fitting Knight's form (Knight 1969) of the Bertalanffy equation.

A method is described here in which (a) the range of application of the model can be observed and tested statistically and (b) the Bertalanffy parameters can be estimated with confidence limits.

Derivation and Method

The Bertalanffy growth model can be expressed differentially in terms of length as follows:

$$(1) \qquad \frac{dl}{dt} = K(L\infty - l)$$

The instantaneous growth rate, G, can be expressed in the form

$$G = \frac{d(\log_e w)}{dt}$$

The weight–length relationship, $w = al^b$, is expressed in logarithmic form and differentiated with respect to time.

$$\frac{d(\log_e w)}{dt} = b\,\frac{d(\log_e l)}{dt} = \frac{b}{l}\frac{dl}{dt}$$

and is substituted into the equation for G

$$(2) \qquad G = \frac{b}{l}\frac{dl}{dt}$$

For the length (or age) range to which the Bertalanffy model applies, G can be expressed in terms of K, $L\infty$ and l by substituting (1) in (2)

$$(3) \qquad G = bK\left(\frac{L\infty}{l} - 1\right)$$

Therefore, a plot of G vs. the reciprocal of length should produce a straight line of slope $bKL\infty$ which intercepts the G axis at $-bK$ and the $1/l$ axis at $1/L\infty$ (when $G = 0$ by definition). The important fact about this equation is that the variables can be measured independently. G is measured from weight increase in time and plotted against the reciprocal of the mean length over which G has been estimated. A predictive rather than a GM functional regression (Ricker 1973) is recommended because $1/l$ should normally be much more accurate and subject to less natural variability than G. Any dependency of G on $1/l$ can be observed graphically and tested statistically.

An estimator for K and its variance can be found as follows:

$$\hat{K} = \frac{\widehat{bK}}{\hat{b}}$$

The intercept bK is estimated from the regression of G on $1/l$, and b from weight–length measurements. $\widehat{bK}$ and $\hat{b}$ can be assumed to be independent. Consequently, the variance of $\hat{K}$ can be estimated as follows:

$$\mathrm{Var}\,(\hat{K}) = \frac{1}{b^2}\mathrm{Var}\,(\widehat{bK}) + b^2K^2\,\mathrm{Var}\,(1/\hat{b}) + \mathrm{Var}\,(\widehat{bK})\,\mathrm{Var}\,(1/\hat{b})$$

In practice the last term is negligible, because of the relatively small value of $\mathrm{Var}(1/\hat{b})$. In Example 1 (below) it was 0.06% of $\mathrm{Var}(\hat{K})$. It is convenient to obtain the estimate of $\mathrm{Var}(1/\hat{b})$ using the GM regression of $\log_e l$ on $\log_e w$ rather than the reverse. Thus, the estimate of b will be the reciprocal of the regression coefficient providing the GM regression is used. The "between age-group b" of Ricker (1975, p. 221) is recommended.

Confidence limits of $1/L\infty$, hence $L\infty$, can be obtained using the method of Snedecor and Cochran (1973, p. 159).

It should be added here that the von Bertalanffy model is used as a purely empirical relationship in terms of length. The physiological arguments involved in its derivation, in which a value of $b = 3$ is assumed, do not have to apply in this case.

Example 1

Growth of ciscoes from Vermilion Lake, Minnesota (data from Carlander 1950)

These data have been presented and analyzed using various methods by Ricker (1975, p. 226–228). Results of a reanalysis using the Walford plot and the Beverton method are presented here. These are compared with the computer results (Ricker 1975, p. 228) and those from the method described here.

TABLE 1. Results of regressions of G on $1/l$ for ciscoes from Vermilion Lake, Minnesota (data from Carlander 1950). CL = confidence limits.

Age range	r	Regression coeff. ($= L\infty\, bK$)	Intercept when $1/l = 0$ ($= -bK$)	$K \pm 95\%$ CL	$L\infty$ (mm) $\pm$ 95% CL
3–9	0.9811	0.3845	$-1.2653 \pm .3941$	0.432 ± 0.135	304^{+35}_{-23}
3–11	0.9848	0.3836	$-1.2616 \pm .2463$	0.422 ± 0.086	304^{+21}_{-17}
2–10	0.9916	0.3467	$-1.1279 \pm .1771$	0.377 ± 0.063	307^{+27}_{-21}
2–11	0.9920	0.3495	$-1.1409 \pm .1529$	0.382 ± 0.056	306^{+24}_{-20}

Figure 1 shows the plot of G vs. $1/l$ for all data presented. G was calculated from the difference between natural logarithms of the mean weights of consecutive ages, and $1/l$ is the reciprocal of the arithmetic mean of the two average standard lengths presented. It could be argued that the geometric mean is appropriate, but in practice the effect on the parameter estimates is negligible.

The parameters derived estimate growth of the population. A straight line relationship is clear from Fig. 1, and Table 1 shows predictive regressions calculated from various combinations of the points. The "between age-group b" was estimated to be 2.990 from ages 2 to 10 using the GM regression, and the estimate of $\mathrm{Var}(1/\hat{b})$ was 0.000068.

Table 1 and Fig. 1 clearly show that there is no reason statistically for rejecting any of the points, and I would prefer the last estimate (ages 2–11) if random variability is the most important source of error. This is the line shown in Fig. 1.

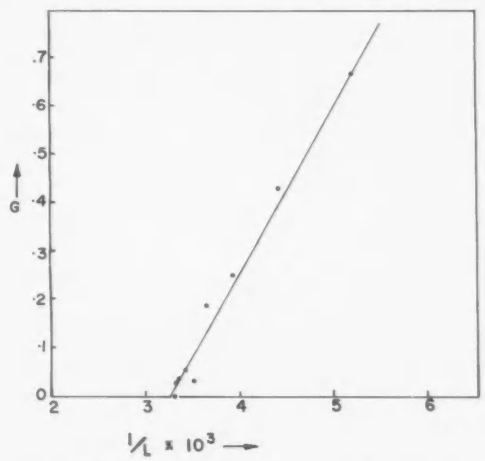

FIG. 1. G vs. $1/l$ plot for ciscoes from Vermilion Lake, Minnesota (data from Carlander 1950) with least squares regression line for ages 2–11.

Analysis using the Walford plot (GM regression) and the best-fitting Beverton (1954) plot were made, and the results are shown in Table 2, along with two selected from Table 1, and those from Ricker (1975, p. 228) using Allen's VONB program.

The t_0 values for the Walford and G vs. $1/l$ methods are unweighted means for ages 3–8 using the following formula rearranged from that of von Bertalanffy:

$$t_0 = t + \frac{1}{K}\log_e\left(\frac{L\infty - lt}{L\infty}\right)$$

and the confidence limits of those means are also shown in Table 2. These values are therefore rough estimates from an arbitrary age span, and better estimates may be possible with more information from the population (Gulland 1964, p. 38).

The alternative method (Beverton 1954) of estimating t_0 (and K) by plotting $\log_e((L\infty - l_t)/L\infty)$ against t is not recommended. The reason for this should be apparent from the regressions for various values of $L\infty$ shown in Table 3. Any of these plots produce highly significant correlations, yet a 5% increase in $L\infty$ produces a 166% reduction in t_0 and a 43% reduction in K. The supposedly best regression produces a K value significantly lower than the other methods (Table 2) and the t_0 value appears rather small.

Example 2

Growth of bluegills from Muskellunge Lake, Indiana (Ricker 1958, 1975)

This example was chosen because (a) growth

TABLE 2. Comparison of methods of estimating K, $L\infty$, and t_0 for ciscoes from Vermilion Lake, Minnesota (data from Carlander 1950).

Method	Ages	Weighting	$K \pm 95\%$ CL	$L\infty \pm 95\%$ CL	$t_0 \pm 95\%$ CL
Walford plot (GM regression)	3–9	No	0.370	311	−0.08± .14
Beverton (1954)	3–9	No	0.318± .029	317	−0.52
Computer, VONB (Allen 1967)	3–9	No	0.389	310	+0.105
" " "	3–9	Yes	0.407	309	+0.252
" " "	3–11	No	0.407	308	+0.201
" " "	3–11	Yes	0.414	308	+0.292
Regression G on $1/l$	3–9	No	0.423±0.135	304^{+35}_{-23}	+.08± .17
"	2–11	No	0.382±0.056	306^{+24}_{-20}	−.31± .24

TABLE 3. Values of K and t_0 for various $L\infty$ values using Beverton's method for Vermilion Lake ciscoes (ages 3–9) (Data from Carlander 1950).

$L\infty$	r	$K \pm 95\%$ CL	t_0
305	−0.9772	0.529±0.132	+1.10
307	−0.9888	0.464±0.080	+0.70
309	−0.9938	0.420±0.054	+0.38
311	−0.9960	0.386±0.040	+0.11
313	−0.9969	0.360±0.033	−0.13
315	−0.9971	0.337±0.030	−0.35
317	−0.9968	0.318±0.029	−0.52
319	−0.9963	0.301±0.030	−0.73

data for time periods less than one year are presented and (b) the younger ages show a typical departure from the Bertalanffy model found in many other populations.

Figure 2 shows the plots of G *vs.* $1/l$ for ¼-yr (the "year" being the "growth year" of 6 mo) intervals, and those for yearly intervals. The 4¼-yr G values are 4 times those presented in Ricker (1975, table 10.3) to standardize the units to yr^{-1}. The plot is linear at ages more than 2¾ growth years, but at lesser ages a departure from the Bertalanffy model is evident. This is evident from both the quarterly and yearly plots.

However, if one observes the Walford plots in Fig. 3, a departure is not evident from the quarterly data, and only a slight departure is suggested in the yearly plots. In addition, the departure of points from a regression cannot be tested statistically from the Walford plot, whereas this is possible (although not necessary in this example) in the G vs. $1/l$ plot using a method described by Snedecor and Cochran (1973, p. 157).

The results of various regressions are presented in Table 4. The weights used to calculate G were estimated from the mean lengths using the "year-class b" and therefore G is not strictly independent from $1/l$. However, the plot in Fig. 2 is

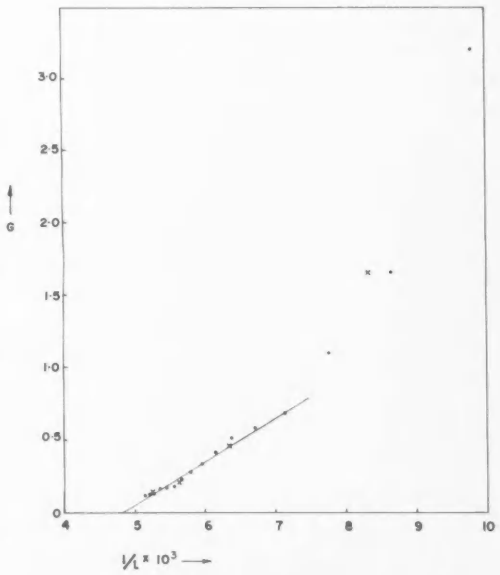

FIG. 2. G vs. $1/l$ plot for bluegills in Muskellunge Lake, Indiana (Data from Ricker 1975, p. 242–243). Solid circles are quarterly measurements and crosses are yearly measurements.

typical of many fish populations even though the confidence limits derived may not be very meaningful in this example.

"Year-class b" was estimated to be 3.511, but since no confidence limits could be estimated, those shown for K in Table 4 assume that all the error of the intercept $-bK$ is due to K. The t_0 value is the unweighted mean for ages 3–6 calculated as in Example 1.

Table 4 clearly shows that consistently lower values of K and t_0 are obtained from the G vs. $1/l$ plot than from any of the Walford plots, and the latter show considerable variation in all three

TABLE 4. Comparison of methods of estimating K, $L\infty$, and t_0 for bluegills in Muskellunge Lake, Indiana (from Ricker 1975, p. 241–243).

Method	Growth increments used	Min age of series analyzed (in growth years)	r	K	$L\infty$ (mm)	t_0
G vs. $1/l$ plot	quarterly	$2\frac{3}{4}$	0.9935	0.42 ± 0.04	207^{+8}_{-7}	$-0.29\pm.18$
Walford	quarterly	$2\frac{3}{4}$	0.9994	0.56	206	$+0.86\pm.03$
Walford	quarterly	2	0.9996	0.58	206	$+0.98\pm.03$
G vs. $1/l$ plot	annually	3	0.9939	0.42 ± 0.57	207	$-0.34\pm.67$
Walford	annually	3	0.9996	0.47	211	$+0.52\pm.02$
Walford	annually	2	0.9959	0.60	204	$+0.95\pm.18$

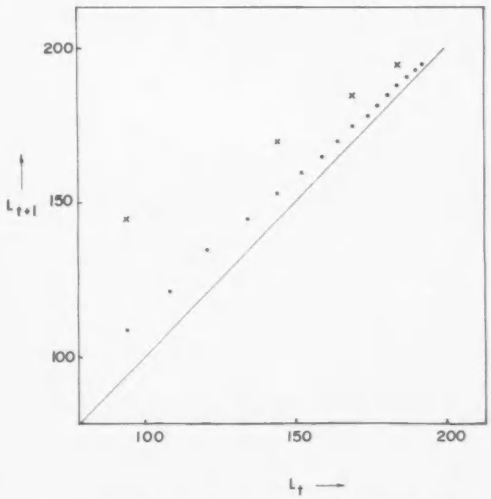

FIG. 3. Walford plots for bluegills in Muskellunge Lake, Indiana (data from Ricker 1975, p. 242–243). Solid circles are quarterly measurements and crosses are yearly measurements.

parameters. Moreover the consistently high correlation coefficients (used here merely to show proximity of the points to a straight line) make the choice between Walford plots more difficult.

General Conclusions

The method described here has the following advantages over the Walford or Gulland plots:

1) The variables can be measured independently allowing (a) statistical determination of limits of application of the Bertalanffy model and (b) estimates of confidence limits of the parameters.

2) Graphical representation of conformity with the Bertalanffy model is clearer.

3) Unequal and/or overlapping time intervals can be used for estimating G, providing that bias is not introduced and that the intervals are not too long.

4) It is possible to compare statistically Bertalanffy growth parameters between populations or between individual and population estimates within a population.

To obtain independent measurements of G and $1/l$ weights and lengths should be measured on aged fish. Large numbers of weight–length measurements should be taken independently to estimate b (preferably "year-class b") over the appropriate age range. These are not considered restraints on the applicability of the method, since fishery investigations normally require large samples of these measurements.

When back calculations from scale (or other hard part) annuli are employed, it is recommended that a functional regression of log (weight) on log (scale radius) be obtained for G estimates.

A potentially useful application is in situations typical of some tropical species where individuals cannot be aged, but growth is estimated from recapture of marked fish. In this case, it is often not possible to control time between release and recapture. However, if growth varies seasonally, weighting of the data may be necessary.

As with other methods individual and population growth parameters can be estimated from appropriate data, but with the added advantage that statistical comparisons may be possible providing that the variance of the individual G estimates is not too high.

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Repeat Homing of Brown Trout (*Salmo trutta*) in Lake Eucumbene, New South Wales, Australia

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TILZEY, R. D. J. 1977. Repeat homing of brown trout (*Salmo trutta*) in Lake Eucumbene, New South Wales, Australia. J. Fish. Res. Board Can. 34: 1085–1094.

Spawning runs of lentic-dwelling brown trout (*Salmo trutta*) and rainbow trout (*S. gairdneri*) in Swamp Creek, an inlet of Lake Eucumbene, were studied for 4 consecutive yr, and 3517 browns and 415 rainbows were tagged during 1968–70. A further 240 browns and 229 rainbows were marked in other inlets. Recaptures of marked browns in 1969 and 1970 showed a high incidence of repeat homing, up to 25.7 and 10.6% returning after 12 and 24 mo, respectively. Few rainbow trout homed. Tag loss and the mortality and maturation of marked browns were estimated and percentage homing and straying in 1969, 1970 and 1971 was calculated. High percentage homing (≥90%) in 1969–70 and the variance in external form in the lentic population suggested some genetic isolation within the brown trout population. Homing ability was not influenced by fish age. Percentage homing fell markedly in 1971 after the removal of nearly all resident brown trout from Swamp Creek and suggested racially distinct stream trout populations to be an important navigational cue to homing brown trout.

Key words: repeat homing, *Salmo trutta*, homing frequency, navigation, racial cue, Australia

TILZEY, R. D. J. 1977. Repeat homing of brown trout (*Salmo trutta*) in Lake Eucumbene, New South Wales, Australia. J. Fish. Res. Board Can. 34: 1085–1094.

Nous avons étudié durant 4 a consécutives les montaisons de fraie de truites brunes (*Salmo trutta*) et de truites arc-en-ciel (*S. gairdneri*) vivant en eaux dormantes dans la crique Swamp, une petite baie du lac Eucumbene, et nous avons marqué 3 517 truites brunes et 417 truites arc-en-ciel en 1968–70. Nous avons marqué de plus 240 truites brunes et 229 truites arc-en-ciel dans d'autres petites baies. Les recaptures en 1969 et 1970 de truites brunes marquées révèlent une forte incidence de homing répété, jusqu'à 25.7 et 10.6% revenant après 12 et 24 mo respectivement. Peu de truites arc-en-ciel retournèrent à leur lieu d'origine. Nous avons estimé les pertes de marques ainsi que la mortalité et la maturation des truites brunes marquées, et avons calculé le pourcentage de homing et errance en 1969, 1970 et 1971. Le haut pourcentage de homing (≥90%) en 1969–70 et la variance de la forme externe de la population lentique suggèrent tous deux quelque isolement génétique au sein de la population de truites brunes. La capacité de homing n'est pas affectée par l'âge des poissons. Le pourcentage de homing diminua de façon marquée en 1971, à la suite de l'enlèvement de presque toutes les truites brunes résidentes de la crique Swamp. Ceci donne à croire que des populations de truites de cours d'eau de races distinctes sont une aide de navigation importante pour les truites brunes retournant à leur lieu d'origine.

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THIS study describes the repeat homing of spawning brown trout (*Salmo trutta*) in Lake Eucumbene, N.S.W., Australia. The observations were made during studies of brown trout and rainbow trout (*S. gairdneri*) populations within the lake's catchment. An attempt is made to assess quantitatively the incidence of repeat homing as opposed to straying by estimating the number of marked fish failing either to be recognized because of tag loss or to return because of nonmaturation and mortality. The incidence of homing dropped markedly after nearly all resident *S. trutta* were eliminated from the study stream, and the possible role of such residents as a navigational cue is discussed. Marked rainbow trout exhibited a low incidence of homing throughout this study.

The homing of salmonids to specific natal streams is well documented and numerous attempts have been made to elucidate the navigational cues used during such migrations. Most investigations centered on the commercially important Atlantic and Pacific salmons and many of the results are comprehensively reviewed by Hasler (1971).

Observations on homing behavior in trout

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species are fewer. The movements of cutthroat trout (*S. clarki*) in Yellowstone Lake, Wyoming, U.S.A., have been much studied (Jahn 1966, 1969; McCleave 1967; McCleave and LaBar 1972) and homing has been found to occur. Lindsey et al. (1959) observed reproductive homing in Rainbow trout and Shapovalov and Taft (1954) recorded homing in the sea-run, steelhead strain of this species. O'Connor and Power (1973) demonstrated repeat homing by brook trout (*Salvelinus fontinalis*). The reproductive and repeat homing of *Salmo trutta* was observed by Stuart (1957). Thorpe (1974) also showed that adults of this species homed to previously occupied "favorable" littoral areas of Loch Leven, Scotland, after overwintering in other localities.

Quantitative assessments of the incidence of repeat homing as opposed to straying have been limited by the lack of knowledge of marked fish mortality and tag loss, and the impracticability of uniformly monitoring all possible spawning streams.

Materials and Methods

Lake Eucumbene is an artificial impoundment created by damming the Eucumbene River in 1957. It is located near 36°03'S, and 148°43'E at an altitude of 1164 m (Fig. 1). At full supply level the lake's volume is 4.8 km^3 and its surface area 145 km^2. Two trout species, *S. trutta* and *S. gairdneri*, occur throughout most of the catchment, having been introduced in the late 19th century. The stream-spawning lentic trout populations have access to all major tributaries except two with insurmountable physical barriers (Fig. 1). This study centered on Swamp Creek (Fig. 1) which has a total length of 10.5 km, comprising 6.6% by length of the streams accessible to spawning trout.

All spawning trout sampled in Swamp Creek were taken in a fixed upstream trap similar to that described by Munro and Balmain (1956). Spawners from other tributaries were caught in drum-nets or rigid weldmesh traps of similar design. Fish captured were examined for species, sex, weight, fork length, and the presence of tags or tag scars; 10-20 scales were removed from most specimens for age analysis. All fish tagged in 1968 and 1969 were aged, except a few with unreadable scales. Traps were emptied daily throughout the 1969 and 1970 spawning seasons. Fish were removed from the trap, anesthetized in a 20 mg/ℓ quinaldine solution, examined as above, tagged, briefly immersed in a 5% solution of malachite green to minimize posthandling infection and placed in canvas pools to revive before being released below the trap. In 1968 and 1970 a 4-g monel-metal strap tag was affixed to the posterior edge of the left operculum as dorsally as possible. Many fish were double tagged (one tag on each operculum) to ascertain the rate of tag loss. In 1969 the "Floy FD-67" tag was inserted between the neural rays of the dorsal fin

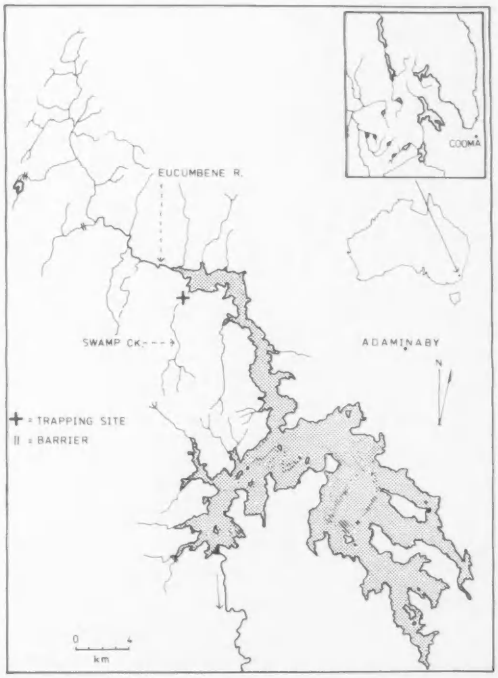

FIG. 1. Lake Eucumbene at full supply level and its feeder streams. The natural barriers shown deny access to spawning trout.

(Dell 1968). Some anchor-tagged fish were also tagged on the right operculum to avoid confusion with 1968 single-tagged fish. Ripe fish were stripped before tagging in 1968 and 1970 to facilitate a rapid return to lentic waters. Every tagged fish was released in good condition and the 800-m length of Swamp Creek between the trap and the Eucumbene River was inspected daily for dead or ailing fish. All trout not used in the tagging experiments were released above the trap after being measured, except for a few killed for fecundity measurements and gut-content analyses. In 1969 the entire run was released above the trap after examination, and spent downstream migrants in good condition were the only fish marked.

Just before the 1971 spawning season, Swamp Creek and its tributaries were rotenoned from approximately 9 km upstream of its junction with the Eucumbene River to eliminate resident adult and juvenile brown trout. The main objective of the poisoning was to allow the spawning of only rainbow trout in Swamp Creek during the 1971 winter, as part of an interspecific (rainbow: brown) behavioral study. A weldmesh barrier was then immediately constructed across the creek just above the 1968–70 trapping site to prevent lentic brown trout from gaining access to spawning areas. Brown trout accumulating below this barrier were regularly caught by electrofishing at

intervals of 3–5 days, and all unmarked fish were killed. Trapping commenced at the start of the rainbow trout run (August 5, 1971) and continued until the finish of the brown trout run (September 4, 1971) when trap and barrier were removed. Not all lentic brown trout entering Swamp Creek in 1971 were caught but 1573 fish were taken and examined as in previous years.

Tagging was primarily aimed at estimating the size of the lentic populations, and lentic recoveries were via the amateur sport fishery. Simultaneous studies (Tilzey unpublished data) into the dynamics of the lake's trout populations provided estimates for total annual mortality and percentage maturation in each year-class. Swamp Creek was also the site of several other studies, from which data are occasionally quoted.

Results

A total of 3757 brown trout were tagged and released during the 1968, 1969, and 1970 winters (Table 1). Rainbow trout were not as abundant and only 644 were tagged in 1968–69. As this study centers on Swamp Creek, trout marked elsewhere are grouped together for convenience (Table 1), most such fish being taken from the Eucumbene River. Angling returns of marked fish recaptured from a known locality showed them to occur throughout the lake. Most fishing effort and recaptures occurred in the littoral zone and close to marinas with accommodation complexes catering to amateur fishermen. Recaptures revealed little correlation between the distance moved by marked fish and the time elapsed since release. Catch distribution patterns for brown trout marked in 1968, 1969, and 1970 and rainbow trout marked in 1968 and 1969 were very similar and marked fish were observed to be dispersed through lentic waters before and after reproductive migrations.

In 1968, 1969, and 1970 the entire spawning runs entering Swamp Creek totaled 2538, 2862, and 3525 browns, and 407, 590 and 294 rainbows, respectively. Both runs were subsampled in 1971 and 1573 browns and 94 rainbows were caught.

In 1969 and 1970 a much greater percentage of brown trout previously marked and released in this creek returned to spawn than did brown trout marked elsewhere (Table 2). Fish that lost opercular tags were easily recognized by a distinct, groove-shaped erosion in an operculum. The low

TABLE 1. Summary of fish marked 1968–70 by species, sex, fork length (F.L.) range, and locality. OP = Opercular strap tag; FD67 = Floy Anchor tag.

Winter	Locality	No. marked: By sex	No. marked: Total	F.L. range (mm)	Tag type
		Brown trout			
1968	Swamp Cr.	M 525	1302	306–555	OP
		F 777		314–537	OP
	Elsewhere	M 44	190	321–525	OP
		F 146		320–530	OP
1969	Swamp Cr.	M 128	470	264–556	FD67
		F 342		293–542	FD67
	Elsewhere	M 11	50	323–546	FD67
		F 39		361–500	FD67
1970	Swamp Cr.	M 702	1745	256–611[a]	OP
		F 1043		297–570	OP
	Elsewhere		Nil		
		Rainbow trout			
1968	Swamp Cr.	M 175	297	325–536	OP
		F 122		367–544	OP
	Elsewhere	M 71	135	353–548	OP
		F 64		374–525	OP
1969	Swamp Cr.	M 49	118	262–511	FD67
		F 69		380–550	FD67
	Elsewhere	M 21	94	345–486	FD67
		F 73		405–535	FD67

[a]Excluding one atypically large specimen of 730 mm.

TABLE 2. Summary of marked fish recaptures in Swamp Creek only. Year marked (YM) and release locality (RL): S = Swamp Creek, E = elsewhere.

YM/RL	No. marked	Recaptures: Year	Recaptures: No.	Recaptures: %	Lost op. tag
		Brown trout			
1968					
S	1302	1969	295	22.7	40
E	190		2	1.1	
S		1970	77	5.9	61
E			1	0.5	
S		1971	1	0.1	—[a]
E			0	—	
1969					
S	470	1970	48	10.2	—
E	50		1	2.0	
S		1971	3	0.6	—
E			1	2.0	
1970					
S	1745	1971	23	1.3	26[a]
E	0		—	—	
		Rainbow trout			
1968					
S	297	1969	3	1.0	5
E	135		3	2.2	
S		1970	0	—	0
E			0	—	
S		1971	0	—	0
E			0	—	
1969					
S	118	1970	2	1.7	—
E	94		0	—	
S		1971	0	—	—
E			0	—	

[a]Fish observed to have lost opercular tags in 1971 could not be separated into 1968 and 1970 groups.

return of tagged brown trout marked elsewhere indicated that most, if not all, fish recorded as having lost opercular tags were originally tagged in Swamp Creek. Assuming all such brown trout to have been tagged in Swamp Creek in 1968, the adjusted total recoveries in 1969 and 1970 would be 335 (25.7% of the total 1302 marked) and 138 (10.6%), respectively. Fish having lost anchor tags could not be readily distinguished, as discernible scars were evident on only 3/22 fish known to have lost an anchor tag through being opercular tagged. Recoveries of marked brown trout in 1971 were much lower than in the previous 2 yr, even though a comparatively large number were tagged in 1970. Recoveries of marked rainbow trout were low throughout.

Comparison between 1969 and 1970 records for the Swamp Creek trap showed that 49 of the 78 brown trout bearing 1968 tags recorded in 1969 also returned in 1970. The single 1968-tagged brown trout "stray" recorded in 1970 was one of the two "strays" recorded in 1969. In 1971 the one recorded brown trout tagged in 1968 had not previously returned to Swamp Creek in 1969 and 1970, and of the three recorded brown trout tagged in 1969 only one had previously returned in 1970.

Sporadic trapping elsewhere in the catchment yielded few marked fish. In 1969 two brown trout were captured in the Eucumbene River, both of which were originally tagged there in 1968. Gang Gang Creek, a tributary 1 km from Swamp Creek, yielded two rainbow trout bearing 1968 tags, one originally tagged there and the other in Swamp Creek. In May and June 1971 gill nets set at the mouth of the Eucumbene River captured 16 brown trout originally tagged in Swamp Creek, 3 with 1968 tags, 2 with 1969 tags, and 11 with 1970 tags. The five fish marked in 1968 and 1969 were recorded in Swamp Creek in 1969 and 1970.

Swamp Creek constituted <7% by length of the total spawning waters accessible to the lentic trout populations and its percentage representation by area was undoubtedly lower. The comparatively high returns of marked brown trout in 1969 and 1970 could certainly not be attributed to random upstream migration and it was evident that homing occurred. The low returns of rainbow trout and the comparatively high proportion of straying suggested that homing was much less precise for this species in Eucumbene.

The capture of a few brown trout originally tagged in other streams showed that some straying occurred. The impracticability of simultaneously monitoring all spawning streams within the lake's catchment prevented direct assessment of percentage homing and straying. However, the total numbers of brown trout tagged in 1968 and surviving to spawn again in 1969 can be calculated if mortality of marked fish during the interim period and the percentage maturation of the survivors in 1969 are known. Percentage homing and straying can then be assessed by comparing the estimated total of marked fish surviving and maturing to spawn again in 1969 with the actual number of recaptures in that year, the latter total being adjusted for tag loss. This principle was used to calculate the percentage homing of brown trout marked in 1968 and 1969 to Swamp Creek in 1969, 1970, and 1971, with the following variables being incorporated.

Tag loss: Opercular tag loss did not affect the enumeration of 1968 fish returning to Swamp Creek in 1969 and 1970, except by masking individual recognition. The fish that had lost tags were again aged by scale reading. However, fish observed to have lost opercular tags in 1971 could not be separated into 1968 and 1970 groups.

Anchor tag loss was estimated by examining the 1969 double-tagged fish returning in 1970. Of the 470 brown trout anchor tagged in Swamp Creek in 1969, 200 were also opercular tagged, and 41 of the latter group were recorded in the 1970 Swamp Creek spawning run. Thirty-four fish still retained the right opercular tag, 18 of which had lost the anchor tag; 3 fish had the anchor tag only, and 4 had lost both tags. Anchor tag loss after 12 mo was approximately 50% (i.e. $22/41 = 53.7\%$). Only 3 of the 22 fish known to have lost anchor tags had a scar at the tagging site, and the remaining fish had no discernible mark. This suggested that tag loss had occurred relatively soon after release. The reasons for such a comparatively high initial loss of anchor tags were unclear. Fish known to have lost anchor tags were not included in Table 2 so the number of 1969 brown trout returning in 1970 should therefore be doubled to 96 (20.4%). Examination of fish bearing anchor tags in 1970 showed that 45 of the 48 had the tags firmly embedded and I assumed that tag loss thereafter was negligible. The comparatively high angling returns of such tags in 1970–71 supported this assumption.

Tagging mortality was thought to be negligible, as daily inspections of the length of Swamp Creek between the trap and the Eucumbene River yielded only five dead marked fish in 1968, one in 1969 and three in 1970. These fish were not included in the respective totals. The fish marked were comparatively large (256–611 mm) and the growth of double and single opercular tagged fish of a similar initial size and age did not signifi-

cantly differ. Similar percentages of double- and single-tagged fish returned in subsequent years. Carline and Brynildson (1972) showed the Floy FD-67 tag did not affect the survival of brook trout (*Salvelinus fontinalis*), considerably smaller than the fish described here.

Total annual mortality was calculated from the comparative abundances of each age-group in regular gill and trammel net samplings in lentic waters throughout 1968–72, assuming a constant annual recruitment. Nets used had a stretched mesh size range of 38–152 mm in 12.7-mm increments to minimize bias through size selection, and a total of 4938 brown trout were caught and aged. Data from 1968 to 1972 have been pooled with mean annual mortality estimates given in Table 3. A constant mean annual mortality was thus assumed throughout for each sex and age-group.

Percentage maturation was calculated by examining gonad development in the lentic fish sampled. Brown trout caught over the period December–April, inclusive, were grouped into spawners and nonspawners, with each sex and year-class treated separately. The fish sampled totaled 629 in 1968–69, 749 in 1969–70, and 766 in 1970–71. Mean percentage maturation differed from year to year, being influenced by prevailing environmental conditions, and was thus grouped as separate annual values (Table 4). Maturation values for 2-yr-old fish were undoubtedly inflated as the nets selected the larger fish in this age-group.

Quantitative estimates showed that the great majority of marked brown trout exhibited repeat homing in 1969 and 1970, with few fish straying (Tables 5 and 6). Homing frequencies of the various age-groups returning after 12 mo showed little difference. Calculations for fish tagged in 1969 assumed that the 50% anchor tag loss observed in the 1970 recaptures did not significantly increase thereafter (Table 6). Percentage homing of 1968 and 1969 fish in 1971 was much lower than in the 2 previous yr. However, the single fish bearing a 1968 tag and recaptured in 1971 (Table 5) was possibly accompanied by others that had lost tags and thus become indistinguishable from 1970 fish with opercular scars. The cumulative confidence limit range for the total of spawning fish obviously grows wider with each successive calculation (Tables 5 and 6) and the percentage homing values in excess of 100 reflect this inaccuracy.

Brown trout tagged in 1970 were not aged and thus could not be treated as in Tables 5 and 6. However, their size composition resembled that for fish tagged in 1968 and 1969 except for an

TABLE 3. The total numbers and estimated annual mortality of brown trout in age-groups II–VIII sampled from lentic waters during 1968–72. T.A.M. = Total annual percentage mortality assuming a constant annual recruitment. The figures in parentheses represent 95% confidence limits.

	II	III	T.A.M. III–IV	IV	T.A.M. IV–V	V	T.A.M. V–VI	VI	T.A.M. VI–VII	VII	T.A.M. VII–VIII	VIII	Total
Male	822	921	48.5(±3.2)	474	55.7(±4.5)	210	61.0(±6.6)	82	92.7(±5.6)	6	100.0	0	2515
Female	740	893	46.0(±3.2)	482	52.7(±4.5)	228	67.5(±6.1)	74	91.9(±6.2)	6	100.0	0	2423
Total	1562[a]	1814	47.3(±2.3)	956	54.2(±3.2)	438	64.4(±4.2)	156	92.3(±4.2)	12	100.0	0	4938

[a] Age-group II was obviously incompletely represented.

TABLE 4. Percentage maturation per age-group in the lentic brown trout population 1969–71. CL = confidence limits; N = number sampled.

Age at spawning	Sex	1969 N	1969 % Maturation	1969 95% CL	1970 N	1970 % Maturation	1970 95% CL	1971 N	1971 % Maturation	1971 95% CL
2	M	34	Nil	—	56	14.3	±9.17	60	20.0	±10.12
	F	41	Nil	—	42	Nil	—	40	5.0	±6.75
3	M	86	16.3	±7.80	180	30.0	±6.69	240	37.5	±6.12
	F	66	18.2	±9.3	172	31.4	±6.93	200	29.0	±6.28
4	M	64	34.4	±11.63	62	74.2	±10.89	66	81.8	±9.30
	F	90	83.3	±7.70	86	95.4	±4.42	81	90.2	±6.47
5	M	78	46.2	±11.06	42	71.4	±6.97	32	87.5	±11.45
	F	76	94.4	±5.16	62	90.3	±7.36	22	81.8	±16.12
6	M	40	30.0	±14.20	20	70.0	±20.08	10	80.0	±24.79
	F	38	73.7	±13.99	16	87.5	±16.20	12	91.7	±15.60
7	M	8	75.0	±30.00	6	66.6	±37.73	2	100.0	—
	F	8	50.0	±34.64	5	100.0	—	1	100.0	—

increase in fish within the 260–360 mm range (Fig. 2). This increase was undoubtedly a result of higher percentage maturation in 2- and 3-yr-old fish than in 1969 (Table 4). An attempt was made to calculate the number of brown trout tagged in 1970 that again spawned in 1971. An overall total annual mortality of 60%, similar to that in 1968–70, was assumed. Mortality was probably less when considering the increased proportion of younger fish tagged (Table 3). The calculated 9.2% homing (Table 7) was markedly lower than that in 1969 and 1970 and mirrored the low returns in 1971 of fish marked in 1968 and 1969 (Tables 5 and 6).

All tagged fish returns in 1971 were obviously biased by the incomplete sampling of the Swamp Creek spawning run and were adjusted accordingly. The actual number of spawning brown trout entering Swamp Creek in 1971 was not measured but probably was of the same order as in 1970, as a direct relationship existed between percentage maturation in the lentic population and the numbers of fish in the spawning runs in 1968, 1969, and 1970. In the 1967–68 summer fish samples the overall mean percentage of brown trout maturing to spawn in 1968 was 37.3 (75 of a total of 201 examined) and 2538 fish were trapped in Swamp Creek. Corresponding figures for 1969 were 39.9% maturation (251/629) and 2862 spawners, and in 1970, 49.0% (367/749) and 3525. Overall maturation in 1970–71 was 46.6% (357/766), so the total number of brown trout in the 1971 spawning run was thus probably slightly less than in 1970.

Therefore, the number of fish marked in 1970 and returning in 1971 should be at least doubled to validate comparisons with previous years. However, even if the number of such returns is trebled, the incidence of homing in 1971 was still much lower than in 1969 and 1970. Tables 5, 6, and 7

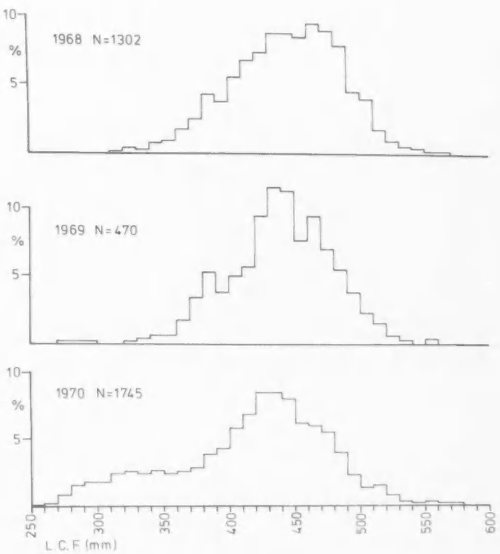

FIG. 2. Percentage length composition, in 1-cm groupings, of the brown trout tagged in Swamp Creek in 1968, 1969, and 1970.

indicate no population dynamics phenomenon which might have caused this drop in homing.

Only two environmental variables differed markedly in the 1971 winter. First, lake level was the highest on record since flooding commenced in 1957. Second, resident brown trout were largely eradicated from Swamp Creek.

Eucumbene's water level has fluctuated continually since 1957. In the 1968 winter the lake was at its lowest level since 1960, after which it rose comparatively steadily until January 1971. Inundation of new ground commenced in November 1969. The Swamp Creek–Eucumbene

TABLE 5. Quantitative estimates of the progressive mortality and annual maturation of brown trout tagged in 1968 and the percentage of total surviving spawners exhibiting repeat homing in 1969, 1970, and 1971. Numbers in parentheses are approximations.

Age	Sex	No. tagged	Annual % mortality	No. survivors	% Maturation	No. spawners	No. retrapped	% Homing
1968								1969
III	M	63	48.5	32	34.4	11	14	100+
	F	107	46.0	58	83.3	48	51	100+
IV	M	273	55.7	121	46.2	56	47	84
	F	395	52.7	187	94.4	177	120	68
V	M	152	61.0	59	30.0	18	17	94
	F	222	67.5	72	73.7	53	69	100+
VI	M	32	92.7	2	75.0	2	4	100+
	F	43	91.9	3	50.0	1	12	100+
VII	M	2	100.0	0				
	F	5	100.0	0				
No age	M	3	(50)	1	(40)			
	F	5	(50)	2	(70)	2	1	
Total	M	525	59.1	215		87	82	94.2
	F	777	58.6	322		281	253	90.0
Total		1302	58.8	537		368	335	91.0
1969		Survivors						1970
IV	M	32	55.7	14	71.4	10	5	
	F	58	52.7	27	90.3	24	31	
V	M	121	61.0	47	70.0	33	12	
	F	187	67.5	61	87.5	53	53	
VI	M	59	92.7	4	66.6	3	1	
	F	72	91.9	6	100.0	6	20	
VII	M	2	100.0	0				
	F	3	100.0	0				
No age	M	1	(60)	0			4[a]	
	F	2	(60)	1	(80)	1	12[a]	
Total	M	215	69.8	65		46	22	47.8
	F	322	70.5	95		84	116	100+
Total		537	70.2	160		130	138	100+
1970		Survivors						1971
V	M	14	61.0	5	87.5	4	0	
	F	27	67.5	9	81.8	7	0	
VI	M	47	92.7	3	80.0	2	1	
	F	61	91.9	5	91.7	5	0	
VII	M	4	100.0	0				
	F	6	100.0	0				
No age	M							
	F	1	(90)	0				
Total	M	65	87.7	8		6	1	16.7
	F	95	85.3	14		12	0	0
Total		160	84.4	22		18	1	5.5

[a]Lost tags and could not be re-aged.

River junction was first submerged during the winter of 1970 and no obvious decline in repeat homing occurred that year.

A series of quantitative samples from Swamp Creek during 1969–71 showed the mean population composition of fish aged 1 yr and above to be 97.8% brown trout and 2.2% rainbow trout, with no other species present (Tilzey 1976). Such sampling also showed that juvenile rainbow trout vacate this creek at a very early age. For example, rainbows comprised only 0.6% of the 0+ aged trout sampled in December 1969, 6–8 wk after the rainbow spawning run ended. The estimated numbers of brown trout in the entire creek on

TABLE 6. Quantitative estimates of the progressive mortality and annual maturation of brown trout tagged in 1969 and the percentage of total surviving spawners exhibiting repeat homing in 1970 and 1971. Numbers in parentheses are approximations.

Age	Sex	No. tagged	Annual % mortality	No. survivors	% Maturation	No. spawners	No. retrapped		% Homing
							Actual	Estimated[a]	
1969									1970
III	M	18	48.5	9	74.2	7	4	8	100+
	F	39	46.0	21	95.4	20	5	10	50
IV	M	32	55.7	14	71.4	10	0	0	0
	F	125	52.7	59	90.3	53	14	28	53
V	M	56	61.0	22	70.0	22	3	6	40
	F	109	67.5	35	87.5	31	16	32	100+
VI	M	19	92.7	1	66.6	1	1	2	100+
	F	51	91.9	4	100.0	4	4	8	100+
VII	M	2	100.0	0					
	F	11	100.0	0					
Not aged	M	1	(50)	0					
	F	11	(50)	5	(70)	3	1	2	
Total	M	128	64.1	46		33	8	16	48.5
	F	342	64.0	124		111	40	80	72.1
Total		470	64.0	170		144	48	96	66.7
1970		Survivors							1971
IV	M	9	55.7	4	87.5	3	0	0	
	F	21	52.7	10	81.8	8	3	6	
V	M	14	61.0	7	80.0	6	0	0	
	F	59	67.5	19	91.7	17	0	0	
VI	M	22	92.7	2	100.0	2	0	0	
	F	35	91.9	3	100.0	3	0	0	
VII	M	1	100.0	0					
	F	4	100.0	0					
Not aged	M	—							
	F	4	(60)	2	(90)	2	0	0	
Total	M	46	71.7	13		11	0	0	0
	F	123	72.4	34		30	3	6	20.0
Total		169	72.2	47		41	3	6	14.6

[a]Assuming a 50% tag loss.

TABLE 7. Estimated percentage of brown trout tagged in 1970 and exhibiting repeat homing in 1971.

Sex	No. tagged	Annual % mortality	No. survivors	% Maturation	No. spawners	No. retrapped			% Homing
						Tagged	Lost tag	Total	
M	702	60.0	280	70	196	12	7	19	9.7
F	1043	60.0	418	80	334	11	19	30	9.0
Total	1745	60.0	698		530	23	26[a]	49	9.2

[a]Possibly includes some fish tagged in 1968.

March 18, 1970 were as follows for each age group:– 0+ 59,800, I+ 28,200, II+ 3,260, together with 460 older fish. Thus, a large number of resident brown trout were removed from this creek by the 1971 rotenone treatment and their absence apparently resulted in much lower repeat homing by lentic brown trout in the 1971 winter.

Brown trout spawning in Swamp Creek in 1969–70 were quite monotypic in appearance, being predominantly deep bodied and brown with moderate red spotting. However, the lentic population exhibited a marked variance in external form and coloration, the fish types ranging from the slender-bodied "loch leven" form with an

overall silver coloration virtually devoid of red pigmentation to the deep-bodied form, dark to light brown in color, profusely covered with red spots and with a bright red adipose fin. This suggested that the high percentage homing in Swamp Creek observed before 1971 had possibly resulted in some genetic isolation. Nevertheless, moderate straying would maintain a degree of genetic homogeneity as numerous spawning creeks exist (Fig. 1). Conversely, the lentic rainbow trout population, which exhibited much lower homing than brown trout, presented a uniform external appearance throughout, being relatively lightly spotted and an overall silvery green in color with a light magenta stripe laterally.

Discussion

This study confirmed the ability of brown trout to home to specific streams and demonstrated their high accuracy and low incidence of straying. Although no juvenile trout were marked in Swamp Creek the observations of Stuart (1957) suggested that the adult brown trout spawning therein had returned to their natal stream. The high degree of homing evident in Eucumbene probably effected a degree of genetic isolation within the lentic population. No morphometric measurements such as those taken by Vernon (1957) were made in this study but Nicholls (1961) found significant differences in meristic features between the brown trout from the Plenty River, Tasmania, and those from the nearby Great Lake, and suggested that they indicated a genetic separation between the two stocks. All brown trout on the Australian mainland are derived from Tasmanian stocks, initially introduced from England in 1864 (Roughley 1951).

Age analysis of marked fish showed no evidence of increasing homing ability with age and suggested that the ability to recognize Swamp Creek was either innate or imprinted at an early age. The reproductive homing of anadromous salmonids which vacate natal streams at an early age is well known and it is generally agreed that the ability to recognize specific streams is present early in life. Stuart (1957) also showed this to be so for nonanadromous brown trout and Lindsey et al. (1959) for rainbow trout. All salmonid species in Australia have been introduced and the ability of Eucumbene brown trout to recognize a specific stream would appear to be a characteristic acquired since introduction. However, genetics may play a significant role in stream recognition through providing a distinctive, inherent navigational cue.

The marked drop in repeat homing of brown trout to Swamp Creek in 1971 as compared to 1969 and 1970 appeared to be associated with the virtual absence of resident brown trout in the creek in 1971. Rising lake levels prevailed throughout 1969–71 and if held responsible for trout disorientation should theoretically have had a maximal effect in 1970 when the Swamp Creek–Eucumbene River junction was first submerged. Stuart's (1957) observations suggest that the repeat homing observed in Swamp Creek was in fact reproductive homing. If this was the case the resident brown trout removed from Swamp Creek were genetically distinct from other stream populations within the Eucumbene catchment. The homing fish could well have been distinguishing between a race-specific character of the discrete Swamp Creek population and those of other streams and orientating accordingly.

The results of Sutterlin and Gray (1973) appear to support this hypothesis. The low return of wild, as opposed to hatchery-reared, Atlantic salmon to a hatchery beside the Saint John River led them to doubt the importance of the general attractant effect of young fish. However, if a race-specific character of the hatchery fish differed from that of the same species in the river, the wild fish could have distinguished between the two stocks and oriented accordingly. Transplanting experiments (e.g. Donaldson and Allen 1957; Carlin 1963) suggested that homing salmonids were conditioned as juveniles to recognize the stream of their choice. I could find no evidence of such transplanted salmonids returning to a stream in which other salmonids, of any race or species, were not present during the period of juvenile residence and subsequent return. Nordeng (1971) suggested that the native fish population of a stream provided the dominant attractant to such transplants.

The apparent failure of rainbow trout to home to Swamp Creek could possibly be attributed to the very early age at which their juveniles vacated this stream. The comparative absence of resident rainbows in other spawning streams (Tilzey 1976) suggested that this may be so for most of the lake's inlets.

Whereas no attempt was made in this study to determine the navigational mechanisms involved, the observations of Stuart (1957) on brown trout and Cooper and Hasler (1976) and Cooper and Scholz (1976) on rainbow trout suggest that the navigational cue was olfactory. Homing by olfaction has been conclusively proven for Pacific salmon of the genus *Oncorhynchus* (e.g. Cooper et al. 1976). Furthermore, Døving et al. (1974) showed the char *Salvelinus alpinus* to respond differently to dilute fish odors from four distinct char populations. Therefore, the resident brown trout population of Swamp Creek could possibly

have constituted a race-specific olfactory navigational cue.

While perfect homing and genetic discreteness did not occur in Eucumbene brown trout, available evidence suggested that the population could possibly be evolving in this direction. Rainbow trout comprised the dominant trout species in the upper Snowy River catchment (Lake 1957), of which Eucumbene is a tributary, before the construction of several impoundments by the Snowy Mountains Hydro-Electric Authority. The advent of lentic conditions resulted in an expansion of brown trout populations which now dominate the respective lake catchments. It was evident that the homing behavior of the brown trout studied here had developed since Lake Eucumbene's formation in 1957. If an inherent race-specific character is a major navigational cue, reproductive homing will result in each spawning site's becoming increasingly distinctive, which in turn should result in increasing homing efficiency in successive generations. Such a mechanism could have facilitated the relatively rapid development of homing behavior in Eucumbene brown trout and may be of some significance in the homing behavior of other salmonid species.

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Circulation and Temperature Structure in Large Marine Enclosures

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STEELE, J. H., D. M. FARMER, AND E. W. HENDERSON. 1977. Circulation and temperature structure in large marine enclosures. J. Fish. Res. Board. Can. 34: 1095–1104.

Certain physical measurements intended to shed light on the circulation in large plastic enclosures (60–2000 m^3) induced by the changing environment in which they are moored are described. Layers of dye were generally seen to diffuse vertically although some important advection effects were also observed. Estimates of an average coefficient of turbulent diffusivity yielded values in the range .05–.26 $cm^2 \cdot s^{-1}$.

Measurements taken with recording thermistor chains both inside and outside the enclosures show strong damping of external fluctuations with periods significantly less than 1 day. Various possible sources of mixing energy are considered and it is concluded that thermal forcing through the wall may be significant and could account for the observed range of coefficients.

The significance of the observed mixing and circulation to the ecology of the enclosures is discussed. Of particular importance is the vertical mixing of nutrients that influences phytoplankton sinking rates and thus plays a crucial role in determining variations in algal concentration at different depths.

Key words: mixing, enclosures, controlled ecosystem pollution experiment, circulation, temperature profiles

STEELE, J. H., D. M. FARMER, AND E. W. HENDERSON. 1977. Circulation and temperature structure in large marine enclosures. J. Fish. Res. Board Can. 34: 1095–1104.

Les auteurs décrivent certaines mesures physiques visant à mieux connaître la circulation dans de grandes enceintes de plastique (60–2 000 m^3) déclenchée par l'environnement changeant dans lequel elles sont amarrées. On voit généralement des couches de colorant se diffusant verticalement, bien qu'on observe également quelques effets importants d'advection. Des estimations d'un coefficient moyen de diffusivité turbulente donnent des valeurs allant de .05–.26 $cm^2 \cdot s^{-1}$.

Des mesures prises à l'aide de chaînes de résistance thermique enregistreuses tant à l'intérieur qu'à l'extérieur des enceintes démontrent un amortissement prononcé des fluctuations externes avec périodes nettement inférieures à 1 jour. On considère diverses sources possibles d'énergie causant le mélange, et on conclut que l'échange thermique forcé à travers la paroi peut être important et expliquerait la gamme de coefficients observée.

Les auteurs analysent la signification du mélange et de la circulation observés par rapport à l'écologie des enceintes. On souligne l'importance particulière du mélange vertical d'éléments nutritifs qui influencent les vitesses de sédimentation du phytoplancton et qui jouent ainsi un rôle crucial en déterminant les variations de concentration algale à différentes profondeurs.

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A knowledge of mixing processes is essential in studying the dynamics of planktonic ecosystems. Vertical mixing controls the supply of nutrients from deeper water and determines the distribution of phytoplankton in the upper layers. At the same time, horizontal mixing can disperse patches of phytoplankton forming in these upper layers. These physical factors impose limitations on the interpretation of biological observations. Ideally, we wish to consider a sequence of observations made over a period of time as samples of the

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same population. If the plankton populations were uniformly distributed at some length scale, then this assumption would be tenable for some time scale. Since patchiness occurs at all scales (Platt and Denman 1975) the assumption, in many theories, of a horizontally smooth world is a major inadequacy. The problem concerns not only the limitations of sampling, but the possible importance of horizontal dispersion in controlling the response of the whole system to perturbation (Steele 1976). These difficulties are particularly acute when we want not only to observe plankton populations but also to alter them experimentally to study the effects of added pollutants or nutrient enrichment.

Such studies require the enclosure of volumes of water sufficiently large to contain three trophic levels — phytoplankton, herbivorous copepods, and small predators such as ctenophores or larval fish. Plastic columns have been developed for this purpose (Menzel and Case 1977; Gamble et al. 1977). The dimensions range from 2.5 m diam, 12 m deep to 10 m diam, 30 m deep (Fig. 1). Work with these has been carried out at Saanich, Vancouver Island and at Loch Ewe, Scotland. The smaller bags have been used for experiments on the effects of pollutants and of nutrient enrichment (CEPEX: see Bull. Mar. Sci., 1977).

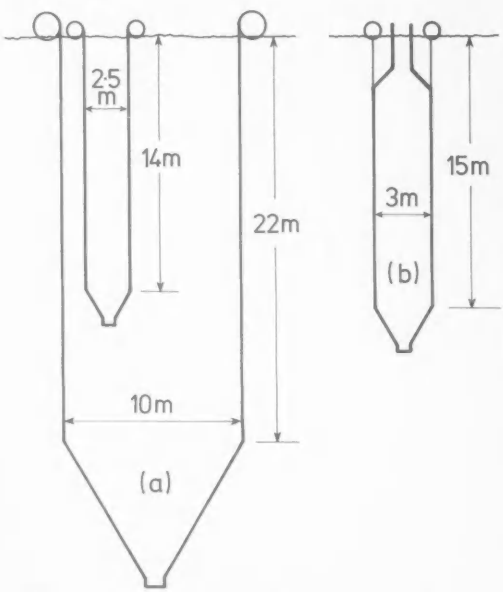

FIG. 1. General design and dimension of plastic enclosures used in plankton ecosystem studies (a) the two sizes used at Saanich, (b) the enclosures used at Loch Ewe.

Experiments with the larger bags are in progress. As part of this work, studies of mixing rates and temperature changes have been made to determine the effect of enclosure on the physical environment within.

Materials and Methods

Rhodamine B dye was used to provide direct observations on mixing. Details of the technique are given in Pritchard (1970). Ten milliliters of a 40% solution of the dye in acetic acid, plus 50 ml distilled water were made up to 1 ℓ with filtered sea water. The full quantity was used to dose a large bag and proportionately smaller doses were used in the smaller bags.

The dye was injected at mid-depths (approximately 5 and 10 m for small and large bags, respectively) using a diffuser ring that gave an initial vertical thickness of about 0.5 m and appeared to spread the dye uniformly in a horizontal direction. Vertical profiles of dye concentration were measured on a Turner fluorometer by continuous flow from a pumped water intake. The hose was lowered at a fixed rate and the delay time measured. During passage of water through the hose, some smoothing occurred and this was determined by injection of a small quantity of dye. The results showed that smoothing would occur up to a scale of 0.3 m.

At Saanich, profiles were made at the center of the bag and at three points about 0.5 m from the wall. At Loch Ewe, because of the bag design (Fig. 1) measurements were made only in the center. The maximum initial dye concentration was usually on the X1 scale of the fluorometer. As the dye spread and diluted, different sensitivities were used. For convenience, the data are presented in terms of the X3 scale of the Turner fluorometer.

Aanderaa thermistor chains were used to provide data on changes with time in the temperature in and out of the bags. For each experiment, a thermistor chain was suspended in the middle of the bag and one outside at a distance of about 0.5 m from the wall. For the experiments in the small bags, chains with thermistors at 2-m intervals were used. For the large bag, a portion of the depth range was covered using 0.5-m intervals. On each occasion, the inside and outside depths were matched as closely as possible. Ten-minute recording intervals were used.

To obtain continuous temperature profiles, a small temperature–depth probe was built for this work, based on a design by Thorpe (Institute of Oceanographic Sciences, Wormley, Godalming, U.K., personal communication). The small size permitted frequent use within the bags, although it was observed that rapidly repeated lowering at the same position created small-scale variability on the record.

Results

Dye Studies

Experiment I, Saanich, August 9–16, 1974 — One hour after injection at 0900, the measure-

ments of maximum concentration at the center and sides were 60, 69, 54, 57 units respectively, and the dye was not detectable beyond ±0.6 m vertically from the maximum. Thus, the center profile (Fig. 2) is representative of the initial conditions. One day later (Fig. 3) there is an increased vertical spread but this is not completely regular or smooth. In particular, the edges display secondary maxima in dye concentration, indicating that mixing cannot be considered as a simple vertical diffusive process. During the succeeding 2 days, a definite secondary maximum developed, and was observed at all four sampling positions (Fig. 4). This second maximum persisted until the end of sampling, at which time the dye was almost uniformly distributed from surface to 9 m where there was a marked discontinuity with no dye penetrating below this depth. The temperature distribution showed no significant feature at 9 m but there may have been a halocline at this depth.

These results have been described in some detail because the observed features are typical of the other dye experiments. They indicate the limitations of describing vertical mixing as a diffusion process. Apparently a description in terms of diffusion does not define the mixing completely but it may be a useful simplification,

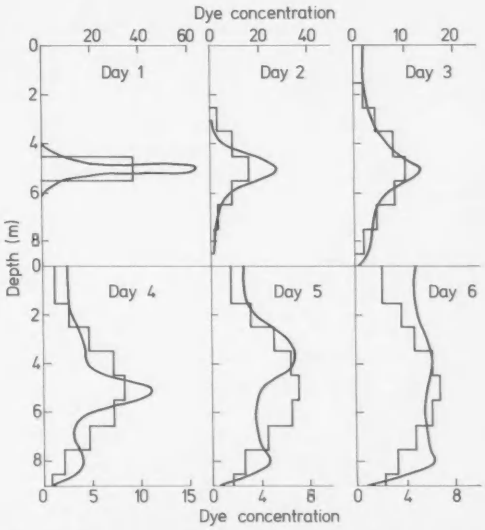

FIG. 2. The continuous curves give the dye profiles at the center of a small bag during a dye experiment in August 1974. The histograms are derived from a simulation model using a coefficient of vertical eddy diffusivity deduced from the observations. (Note changes in the scales for dye concentration).

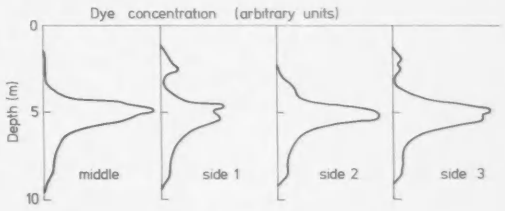

FIG. 3. Dye profiles, 0930–1030, day 2, August 1974 experiment.

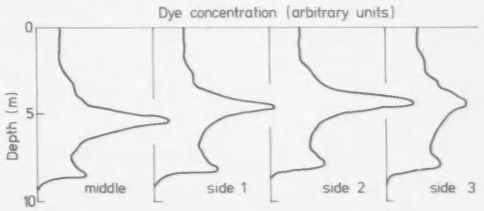

FIG. 4. Dye profiles, 0930–1030, day 4, August 1974 experiment.

particularly for application to simulation models of vertical biological changes.

From the simplest form of the one-dimensional (z-axis) diffusion equation for a conservative scalar of concentration c,

$$\partial c/\partial t = k(\partial^2 c/\partial z^2)$$

and assuming that at time $t = 0$ all the dye is concentrated in a thin layer, then the vertical diffusion coefficient k can be determined through the relation

$$\sigma^2 = 2kt$$

where σ^2 is the variance of the vertical distribution (Csanady 1973). This assumes no boundaries to the dispersion and is an obvious limitation on the application to the data. The variance data for the Saanich 1974 experiment (Fig. 5) yield a range of estimates for k from 0.05–0.1 $cm^2 \cdot s^{-1}$ as an average over time and depth. A 12-layer simulation model of the biological process, with water exchange between the layers (Steele and Henderson 1976) can be adapted to simulate dye diffusion. The output with $k = 0.06$ $cm^2 \cdot s^{-1}$ from 0 to 9 m is given with the initial vertical dye distribution in the layer which is at a depth comparable to that in the bag (Fig. 2). The comparison illustrates the extent to which vertical mixing processes can be represented as turbulent diffusion.

Experiment II, Loch Ewe, June 1975 — In this experiment mixing was much more rapid, giving a faster increase in variance, Fig. 5. The apparent

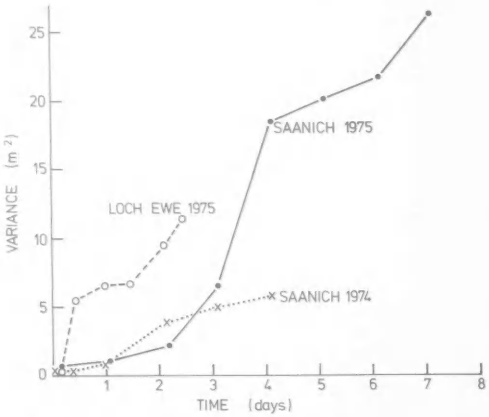

FIG. 5. Variance as a function of time during the three dye experiments.

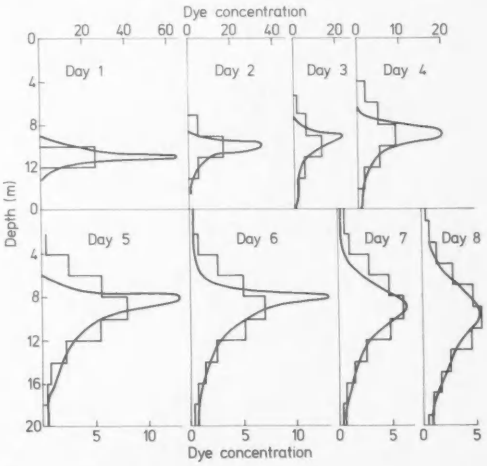

FIG. 6. Dye profiles in Exp. III compared with histograms from the model.

eddy diffusivity coefficient deduced from these observations was approximately 0.26 $cm^2 \cdot s^{-1}$. During these measurements, the difference in density between bottom and near-surface was approximately 0.5 σ_t units while the difference in Saanich bags during Exp. I was close to 1.0. Much of this difference arises from greater thermal gradients in the Saanich area.

Experiment III, Saanich, July 1975 — This experiment was carried out in a large enclosure. In principle, the results did not differ from those obtained in a small bag in 1974. The profiles at the middle and sides were always similar and showed a general vertical spreading with evidence of convective mixing, although this was less marked than for the smaller bag in 1974. The increase in variance over the first three days (Fig. 5) corresponds to a vertical diffusion coefficient of about 0.1 $cm^2 \cdot s^{-1}$. A particular feature of these dye profiles was an upward displacement of the dye maxima with time (Fig. 6). This cannot be due to vertical mixing and must result from vertical advection; such an effect could arise either from transport of fluid from leaks into the bottom and out near the top of the bag, or from distortions in the shape of the bag.

Thermistor Chain Measurements

During July 1974 thermistor data from a bag at Loch Ewe (Fig. 7) computed as hourly means show the response of temperature inside to changes outside. The most noticeable feature of these plots is the considerable smoothing of the higher frequencies during transmission of heat through the wall. Spectral analysis and cross-correlation show that whereas fluctuations in the external temperature series of period much greater than 1 day are transmitted with little change in phase or amplitude, fluctuations much shorter than 1 day are quite strongly attenuated. This suggests that in the present case a time scale of order 24 h is associated with the physical processes responsible for redistributing heat conducted through the bag wall.

A thermistor chain used during Exp. I at Saanich (Fig. 8) shows the same effective filtering action that the bag has on higher frequencies. This feature is emphasized in the amplitude transfer function plot for the 9.5 m records (Fig. 9); for periods less than 12 h there is appreciable attenuation. The 1.5-m values of the amplitude transfer function (Fig. 9) at a period of 1 day will include diurnal heating effects that occur through the surface and so are not transferred through the wall of the bag. Similarly, the outside water at 9.5 m might be expected to receive more of this heat due to downward mixing, which may account for the trough in the amplitude transfer function at this frequency.

Thermistor chains inside the large bag in Exp. III, Fig. 10, show the same general effect but the smoothing of high frequency noise outside appears much greater than for the small bags; longer period effects are not known.

Thermistor Probe Measurements

During Exp. II in Loch Ewe the thermistor probe was used to profile temperature inside the bag and at a distance of 20 m from the bag. The data illustrate the time lapse with reference to outside temperature changes, and the absence of most of the

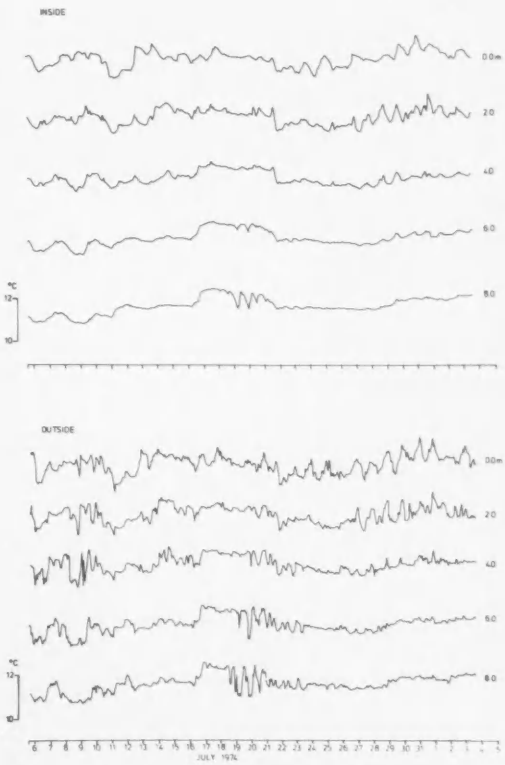

FIG. 7. Hourly mean temperatures outside and inside a bag at Loch Ewe in 1974.

small-scale structures in the vertical temperature distribution which are observed outside (Fig. 11).

Similar measurements were made inside the large bag during Exp. III (Fig. 12a). Initially the outside measurements were made at a distance of only 2 m from the bag wall and showed a marked and rapidly changing fine structure (Fig. 12b). It became apparent that part of this variability arose from disturbances of water flow past the bag. Measurements made 100 m distant from the bag (Fig. 12d) show much less variability but still have significant fine structure compared with the inside.

Discussion

PHYSICAL

Some of the processes that produce mixing outside the bag are inhibited in the enclosed fluid; moreover, some processes that contribute to the mixing may arise from the bag walls themselves. Possible sources of turbulent energy within the bag are:

Surface effects:

(a) wind effects (waves, shear flow instabilities)
(b) convection

Wall effects:

(c) movement of bag wall
(d) thermal forcing

Mechanism (a) is likely to be very small due to the negligible fetch. On the other hand, convection (b) will certainly occur if not inhibited by sufficient salt stratification. Convection is likely to be important during nocturnal cooling and may also be noticeable very close to the surface during the day. Convection during the night in the absence of salt stratification may penetrate to considerable depths.

Movement of the bag walls (c) may arise from wave action on the surface float. Waves in the plastic film are seen to propagate rapidly up and down the wall when the surface float is responding to surface gravity waves and this mechanism may introduce some turbulence to the enclosed fluid. Slower motions associated with distortions of the bag due to outside changes in the vertical density structure have also been observed.

In the absence of strong convection, we consider that thermal forcing (d) may be the most important factor. Changes in the thermal structure

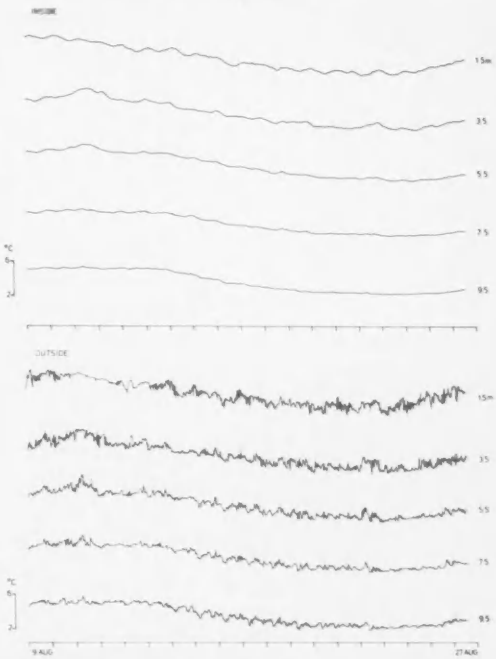

FIG. 8. Ten-minute temperatures during and after Exp. I in Saanich, August 1974.

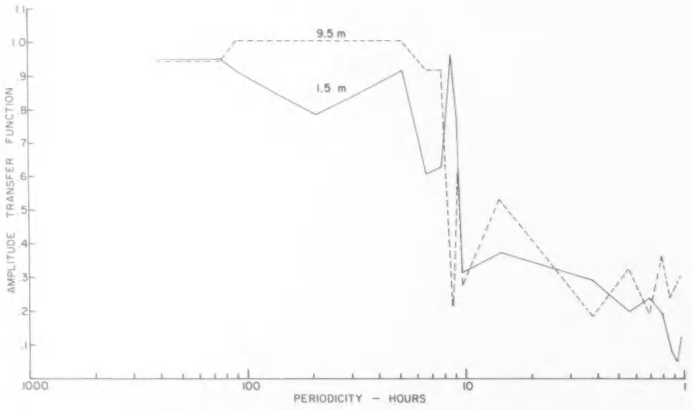

FIG. 9. The amplitude transfer function, T, for the data in Fig. 8 where

$$T(f) = (P_{IN}(f)/P_{OUT}(f))^{\frac{1}{2}}Co(f),$$ and $P_{IN}(f)$, $P_{OUT}(f)$

are the power spectral estimates of inside and outside temperature time series, and $Co(f)$ is the coherence between the two signals at a frequency f.

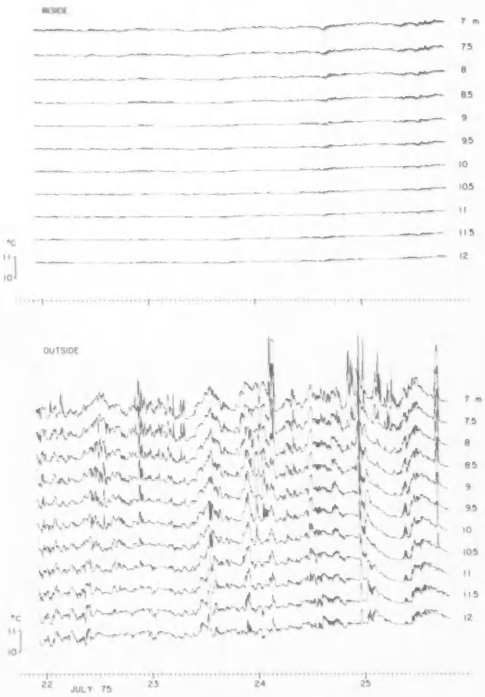

FIG. 10. Ten-minute temperatures during Exp. III.

outside the bag due to wind mixing or internal waves can produce appreciable thermal gradients across the wall. Conduction of heat through the wall may then induce convection within the bag, with consequent mixing.

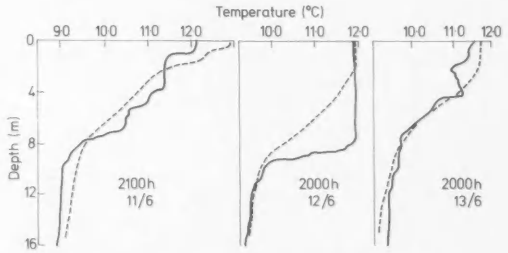

FIG. 11. Temperature profiles on successive days during Exp. II (——— outside; – – – inside).

The thermistor chain data indicate that the internal temperature structure adapts to outside changes with periods of 12 h or more. Boyce (1974), in a theoretical study of mixing in fresh water enclosures (Hesslein and Quay 1973) showed that temperature adaptation could be explained by heat conduction through the wall combined with horizontal mixing, but with only molecular diffusion (10^{-3} cm^2/s) in the vertical. The vertical diffusion coefficients calculated from the dye experiments are about two orders of magnitude greater than molecular diffusion showing that other processes must be operating to induce vertical mixing. Further, the irregularities in dye profiles (Fig. 3 and 4) indicate that these processes are on the vertical scale of metres, suggesting that convection cells are set up in the bag due to temperature changes outside.

The scale of such convection will depend not only on the form taken by the thermal forcing (magnitude of temperature difference across the

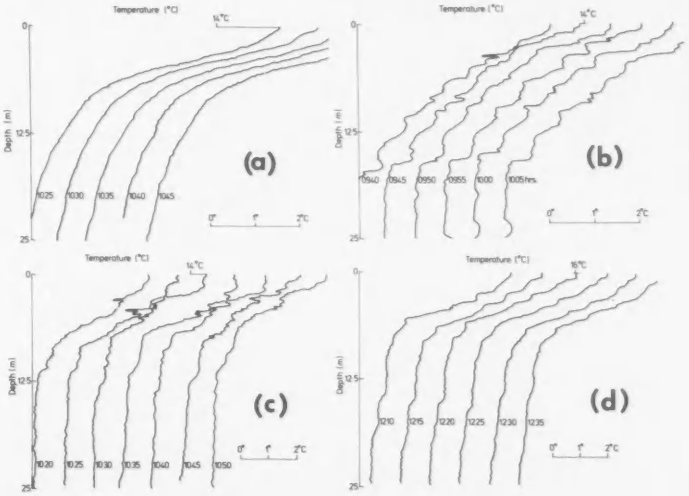

FIG. 12. An example of temperature profiles during Exp. III taken (a) inside, (b) outside at 2 m from the bag on July 21, (c) outside at 0.5 m from bag, and (d) at 100 m from the bag on July 24. (Successive profiles are shifted to the right by an amount equivalent to 1°C.)

wall and vertical motion of isotherms outside the bag) but also on salinity gradients inside the bag. If the salt stratification is not important, the vertical movement of fluid close to the wall would be expected to be comparable to the vertical movement of the isotherms outside, providing the external fluctuations were not too rapid. Continuity would require sinking or upwelling in the interior of the bag. When there is a continuous temperature gradient over the vertical scale of the bags, then a change in temperature could drive convection extending over the full depth of the bag, although of course the actual vertical displacement of fluid particles inside the bag would be limited by the vertical displacement of isotherms outside. With sufficiently large temperature differences across the bag wall, instabilities may set in, producing a series of cells, until equilibrium is achieved.

If salt stratification is important, doubly-diffusive effects may be relevant as shown in the experimental studies of Thorpe et al. (1969) which produced a series of convection cells up a heated side wall. Chen et al. (1971) have shown that the vertical length scale of this layering is close to the height to which a heated fluid element would rise in the initial density gradient. The problem of thermal forcing in the plastic enclosures is more complicated than the laboratory studies, in that the external temperature change is not a simple step-function, but rather fluctuates continuously with perhaps several dominant frequencies. Although the laboratory results are not directly transferable to the present situation they do suggest a means of estimating length scales associated with the resulting convection.

Let r be the fraction by which temperature change contributes to the total density gradient, then this is the fraction of the amplitude of the vertical temperature fluctuation by which a fluid element will rise or fall. If we take this amplitude as a and the period of the temperature change as τ, then the apparent vertical eddy diffusivity k associated with this mechanism only, might be scaled as $k = (ar)^2/\tau$. In Saanich during Exp. I the temperature and salinity gradients were of the order 0.5°C m^{-1} and 0.05‰ m^{-1}, respectively, giving a value of $r = 0.3$ approximately. The maximum vertical excursions of isotherms outside the bag walls during the period August 9–12, was about 2 m, with a period of 20–24 h. Taking a period τ of 20 h, which corresponds to the minimum period temperature fluctuations that were not damped out by the enclosure, gives $k = 0.05$ cm^2/s which is comparable to the value obtained from the dye observations in the region 0–9 m. Further, the lack of any dye penetration below 9 m is consistent with the lack of any rapid short period temperature fluctuations in the bag at that depth (Fig. 8). This correspondence may of course be fortuitous; unfortunately, we have unsufficient data at present to confirm the hypothesis of thermally induced mixing or to estimate the magnitude of effects due to wave induced motions of the bag wall.

In Loch Ewe during Exp. II the amplitude

of temperature fluctuations was comparable to Saanich but the salinity below 2 m contributed slightly to the density gradient. This may explain both the larger vertical mixing coefficient and the relatively smoother dye profiles. Further, there was a marked decrease in dye mixing above 2 m which may be due in part to the salinity gradient, although the constriction of the bag in this region may also have contributed to this effect.

It is to be expected that the effects of heat transfer through the bag wall will be much smaller in the large bags, and this was found to be the case when temperature time series were taken during Exp. III (Fig. 10). The fairly brief time series was quite inadequate to indicate any internal response to external temperature forcing except for a slow drift in temperature. Since the ratio of wall surface to enclosed volume is inversely proportional to radius, the larger bags, having 4 times the radius, would be correspondingly less sensitive to thermal forcing. Further, from the dye measurements, there was an upward displacement of water at a rate of approximately 1 m/day for the first 4 days. The reasons for this are not known, but may be due to a change in shape of the bag which has been observed to occur on other occasions when density differences arise between the water inside and that outside. Such an upward movement inside will produce the same effect as a downward movement of temperature contours outside and this could induce mixing at the same scale.

Thermal forcing of the type discussed above requires appreciable external isotherm movement with periods comparable to or longer than the response time of the bags. In coastal waters such motions might be expected to arise from internal tides, diurnal wind-effects, internal seiches, and similar processes. To determine their possible significance for thermal forcing in a particular location, these effects would first have to be measured and the dominant periods compared with the thermal response time for the bags.

It must be stressed that these proposed mechanisms for mixing inside the bag are very different from those likely to be operating outside. The microstructure outside and the vertical variations in temperature levels indicate a regime of strong internal waves as well as wind-mixing. Thus, although internal waves may be the means of producing vertical mixing inside and outside the bags, they do it in very different ways.

Lastly, the qualitative comparison of dye measurements with eddy coefficients, deduced from possible scales of convective mixing, may provide a basis for the estimation of mixing rates through continuous measurement of temperature and salinity at several depths inside and outside.

Ecological

The ideal environment within the bags compared with outside would have been a marked decrease in the scales of horizontal motion with the rate of vertical exchange remaining the same. Since horizontal and vertical processes are linked, this is theoretically impossible. Vertical mixing within the bags is changed both quantitatively and qualitatively. Effects of the changes in the nature of motions within the bag are demonstrated by the considerable smoothing in vertical temperature profiles. We know (e.g. Fasham and Pugh 1976) that physical microstructure in the natural environment produces corresponding structure in the phytoplankton. In turn, small-scale concentrations of plants may be critical for herbivores feeding on them (e.g. Lasker 1975). The removal of this structure within the bags may be expected to have consequences for the higher trophic levels.

The quantitative decrease in mixing rates, expressed here as eddy diffusion coefficients, will also play a role in determining the vertical distribution of phytoplankton through rates of upward mixing of nutrients and by redistribution of phytoplankton cells produced in the upper layers. The 12-layer model of vertical structure, used earlier for the diffusion calculations, is intended to describe the effects of mixing on plankton populations.

During an experiment in May 1974, marked changes in vertical distribution of phytoplankton occurred (Thomas et al. 1977). The principal feature was the fall-out of large diatoms resulting in an accumulation of chlorophyll near the bottom of the bags (Fig. 13b). Details of the simulation which includes zooplankton are given in Steele and Henderson (1976) and Steele and Mullin (1977). In the May 1974 experiment, zooplankton populations were small and appeared to have a negligible role in determining phytoplankton distribution. This is consistent with ecological studies in nearby Puget Sound (Winter et al. 1975). Apart from mixing, sinking rate will be the main parameter affecting phytoplankton vertical distribution. It is assumed here that this rate, in metres per day, is related to nitrate concentration, N, in the water by

$$V = 2\ (1 - N/20),\ N \leq 20$$

so that there is no sinking at, or above, a nitrate concentration of 20 mg at/m^3; and at zero nutrient, sinking rate has a maximum value of 2 m/day. These features of sinking rate are based on experimental work (Steele and Yentsch 1960; Eppley et al. 1967); the maximum sinking rate corresponds to that for large cells (Eppley et al.

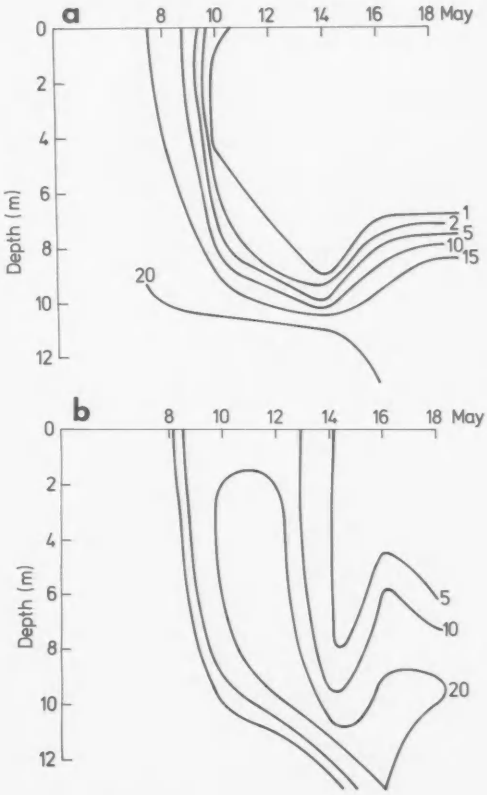

FIG. 13. Observed distributions of (a) nitrate (mg at N/m³) and (b) chlorophyll (mg/m³) during a small bag experiment in May 1974 (from unpublished CEPEX data).

1967) and the value of N = 20 corresponds to the maximum observed concentration in Saanich.

The deduced nitrate (Fig. 14a) shows the same general vertical distribution as the observations (Fig. 13a). For phytoplankton, the output from the model is in terms of particulate organic carbon (Fig. 14b) which shows the main feature of a mid-water maximum. One difference between theory and observation is the shallowing of the observed contours around May 16–18. This might be associated with movement of water within the bag, similar to that observed in the large bag in 1975. This comparison implies that the concentration of large phytoplankton cells near the bottom of the bag resulted from a rapid sinking rate in the upper layers followed by a decreased sinking rate in the nutrient rich deeper waters.

Simulations with increased vertical mixing rates show that nutrients are distributed more uniformly through the water column. This will tend

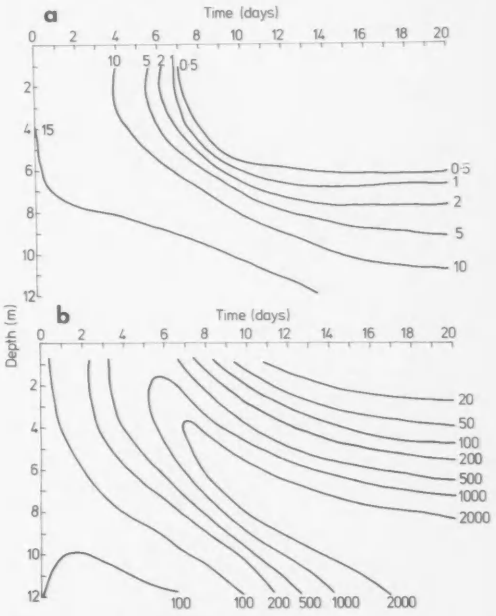

FIG. 14. Theoretical distributions of (a) nitrate (mg at N/m³) and (b) phytoplankton carbon (mg/m³) in a bag with $k = .06$ cm²/s.

to decrease sinking rates in the upper layers but increase them in the deeper water. Thus, phytoplankton are more uniformly distributed with respect to depth, but considerable quantities still fall out into deeper water. Such changes illustrate the complicated interactions between mixing and biological distributions. Manipulations of mixing rates within the bags are required to test such predictions.

Acknowledgments

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Distribution, Abundance, and Resource Utilization of Littoral Zone Fishes in Response to a Nutrient/Production Gradient in Lake Memphremagog[1]

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GASCON, D., AND W. C. LEGGETT. 1977. Distribution, abundance, and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. J. Fish. Res. Board Can. 34: 1105–1117.

The abundance and distribution of six littoral zone fish species (*Notropis volucellus*, *Hybognathus nuchalis*, *Notemigonus crysoleucas*, *Pimephales notatus*, *Fundulus diaphanus*, and *Etheostoma nigrum*) in Lake Memphremagog were influenced directly by a nutrient-driven production gradient existing along the long axis of the lake. The biomass of the six littoral zone fish species was approximately 3 times greater in the more productive southern areas than in the less productive northern areas. Interspecific competition for food was more intense in the less productive northern areas than in the more productive southern areas, and strongly influenced the patterns of food utilization. However, interspecific competition did not appear to play the major role in determining the distribution of the species on the gradient. Distribution of individual species was principally governed by the relative abundance of preferred food resources. The distribution of only one species, *Fundulus diaphanus*, appeared to be determined primarily by direct competition.

Key words: littoral zone, Lake Memphremagog, nutrients, production, resource utilization, fish, food availability

GASCON, D., AND W. C. LEGGETT. 1977. Distribution, abundance, and resource utilization of littoral zone fishes in response to a nutrient/production gradient in Lake Memphremagog. J. Fish. Res. Board Can. 34: 1105–1117.

L'abondance et la distribution de six espèces de poissons (*Notropis volucellus*, *Hybognathus nuchalis*, *Notemigonus crysoleucas*, *Pimephales notatus*, *Fundulus diaphanus*, et *Etheostoma nigrum*) de la zone littorale du lac Memphrémagog sont influencées directement par un gradient de productivité; ce dernier est créé par un gradient en éléments nutritifs qui existe au long de l'axe nord-sud du lac. La biomasse de ces six espèces est environ 3 fois plus grande dans la section sud du lac, plus productive, que dans la section nord. La compétition interspécifique pour la nourriture est plus intense dans la section nord que dans la section sud, plus productive, et elle influence fortement le mode d'utilisation des ressources alimentaires. Par contre, elle ne semble pas être le facteur majeur qui détermine la distribution de chacune de ces espèces le long du gradient. Leur distribution est principalement reglée par l'abondance relative des ressources alimentaires préférées. La distribution d'une seule espèce, *Fundulus diaphanus* semble attribuable principalement à la compétition interspécifique.

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CHANGES in the levels of available nutrients are known to have important influences on lake productivity and on the composition of aquatic communities (Hasler 1947; Beeton 1965, 1969; Colby et al. 1972; Lang 1975; Hickel 1975). Fish populations are thought to be particularly sensitive to production changes at lower trophic levels (Larkin and Northcote 1969). A close relationship between nutrient levels, primary production, and fish production has been demonstrated by several authors (Smith and Swingle 1939; Cross 1950; Smith 1955; Weatherley and Nicholls 1955; Ellis and Gowing 1957; Hall et al. 1970; Tsai 1972; Laurent and Moreau 1973; Nakashima and Leggett 1975). However, the influence of changes in productivity at lower trophic levels on fish community composition is not well understood. Some gross changes in species composition have been attributed to changing nutrient levels (Kriegsmann 1955;

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Regier and Hartman 1973; Christie 1974; Leach and Nepszy 1976), and Nakashima et al. (1977) recently reported changes in the species diversity of the littoral zone fish community of Lake Memphremagog in response to a nutrient/production gradient. However, direct evidence of the relationships between production at primary and secondary trophic levels and fish community composition are rare because of the complicating influence of other factors (physical, chemical, and biological differences between the environments studied, exploitation, species introductions, etc.).

In this investigation we utilized the presence of a strong nutrient/production gradient in a single lake ecosystem to study the relationship between fish community composition and patterns of resource utilization by littoral zone fishes at different levels of primary and secondary production.

Materials and Methods

This study examined the behavior and structure of the littoral zone fish community of Lake Memphremagog (Quebec–Vermont) in relation to the nutrient/production gradient it exhibits. The study concentrated on six species of minnows and darters, since they constitute the only permanent residents of the littoral zone of Lake Memphremagog. The species considered were the mimic shiner, *Notropis volucellus*; the silvery minnow, *Hybognathus nuchalis*; the bluntnose minnow, *Pimephales notatus*; the golden shiner, *Notemigonus crysoleucas*; the banded killifish, *Fundulus diaphanus*; and the johnny darter, *Etheostoma nigrum*.

Lake Memphremagog (Fig. 1) (45°06′N, 72°17′W), is a long (40 km), narrow (mean width 2.4 km) lake of glacial origin located approximately 120 km east of Montreal on the Quebec–Vermont border. It is composed of three morphometrically distinct basins, the characteristics of which are given in Nakashima and Leggett (1975). Its watershed encompasses 1780 km² of which 70% is drained by three rivers, the Black, the Barton, and the Clyde, which enter the lake at a single point at its extreme southern end. These rivers carry agricultural runoff, untreated sewage from several small towns, and sewage effluents from the primary treatment plant of the town of Newport (population about 5000) and discharge them into the Clyde River at its mouth. The three rivers account for approximately 90% of the total nutrient loading of the lake (Kalff and Leggett 1976). Lake Memphremagog discharges at its extreme northern end via the Magog River. Magog, the only other large town in the watershed (population about 15,000) discharges its wastes into the Magog River and thus does not contribute to the nutrient loading of Lake Memphremagog. The virtual point source of nutrients at the inflow results in a pronounced nutrient gradient along the north–south axis of the lake, the steepest portion of the gradient being located in the south basin (Nakashima et al. 1977, Fig. 1). Associated

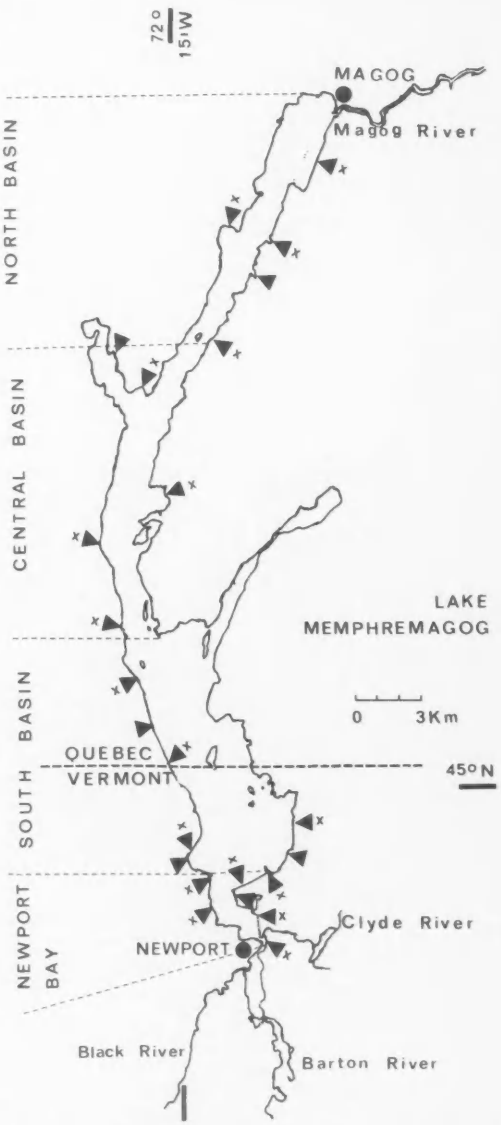

FIG. 1. Lake Memphremagog. ▲, indicate the seine stations sampled in 1974; X, the stations sampled in 1975.

with this nutrient gradient is a gradient in primary production (Ross and Kalff 1975) (ratio south to north 1.25:1), benthic biomass (Dermott 1974) (ratio south to north 2.8:1) and in perch biomass (Nakashima and Leggett 1975) (ratio south to north ≈ 2.5:1). Rooted aquatic vegetation is abundant in the south basin and especially so in Newport Bay at the extreme south end of the lake where it is

TABLE 1. Fish fauna of Lake Memphremagog with a subjective scale of relative abundance (A = abundant; C = common; R = rare; and X = absent). Names follow Scott and Crossman (1973).

Species	Newport Bay	South basin	Central basin	North basin
Hybognathus nuchalis[a]	A	A	C	C
Notemigonus crysoleucas[a]	A	A	C	C
Notropis volucellus[a]	A	A	A	A
Pimephales notatus[a]	A	A	A	A
Fundulus diaphanus[a]	C	R	R	R
Etheostoma nigrum[a]	A	A	C	C
Ambloplites rupestris[b]	R	R	R	R
Lepomis gibbosus[b]	C	R	R	R
Micropterus dolomieu[b]	C	R	R	R
M. salmoides[b]	R	R	R	R
Semotilus corporalis[b]	R	R	C	R
Catostomus commersoni[b]	C	C	R	R
Ictalurus nebulosus[b]	R	R	R	R
Osmerus mordax[b]	R	R	C	C
Esox niger[b]	R	R	R	R
Perca flavescens[b]	A	A	C	C
Notropis bifrenatus	R	R	R	R
N. vornutus	X	X	R	R
Chrosomus neogaeus	R	X	X	X
Couesius plumbeus	R	R	R	R
Salmo salar	R	R	X	X
S. trutta	R	R	R	R

[a]Permanent littoral zone resident
[b]Occasional littoral zone resident

composed mostly of *Vallisneria americana*, *Myriophyllum exalbescens*, *Elodea canadensis*, and *Nuphar variegatum*. Some heavy growths of *Scirpus acutus* also occur along the shore. North of Newport Bay, aquatic vegetation is less abundant and species associations are formed mostly of *V. americana*, *M. exalbescens*, *Potamogeton richardsonii*, *P. amplifolius*, *P. crispus*, and *Nymphaea odorata* (R. Carignan, McGill University, personal communication).

Since the beginning of the multidisciplinary studies of lake production in Lake Memphremagog in 1972, 22 species of fish have been collected of which only 16 occur either commonly or occasionally in the littoral zone (Table 1).

To assess the distribution and abundance of the littoral zone fish species along the nutrient gradient, 24 stations (Fig. 1) were sampled at monthly intervals from May to September of 1974. Twenty additional stations were sampled in June and July to determine more precisely the distributional limits of the silvery minnow and mimic shiner. Sampling was generally performed during the last week of the month and was conducted only during daylight and on days having minimum cloud cover and light winds in order to keep sampling conditions constant. Eighteen of these stations were resampled at 6-wk intervals between May and October of 1975 (Fig. 1). An attempt was made to choose sampling sites having similar physical characteristics. Bottom type varied from fine sand to small gravel and had no correlation with location (north vs. south). Bottom slope was gentle (maximum depth 1–2 m at a distance of 25–30 m from shore), thus ensuring that the full water column was sampled by the seine. The major difference between sites was in the characteristics of the rooted aquatic vegetation which was most abundant in Newport Bay during the summer (in response to high nutrient levels). All stations contained some rooted aquatic vegetation and two northern stations exhibited heavy summer growths. Fish were collected with a bag seine (11.20 × 2.20 m; bag 1.65 × 1.65 × 2 m; 45-mm square mesh). The area sampled by the seine, as used, was approximately 400 m^2. Sampling effort was standardized so that reliable interstation comparisons could be made. All fish collected were killed by suffocation (to avoid food regurgitation) and preserved in 10% Formalin. In some cases, when very large catches were made, a random subsample of 400–500 fishes was killed and the remaining fishes were counted and released. Identification of the species and biomass determinations (to the nearest gram) were done at the laboratory. For statistical purposes, the lake was divided into four areas corresponding to the three morphometric basins and Newport Bay (Fig. 1). Newport Bay was considered as a distinct area because it had been previously shown that the most rapid changes in nutrient concentrations (Kalff and Leggett 1976) and sedimentation rates (G. Spiller, McGill University, personal communication) occurred there. Mean catch per seine haul

(C/UE) of the six littoral zone species studied was calculated for each statistical area and for each sampling interval. Variances in C/UE were proportional to the means indicating nonnormally aggregated populations. Consequently, a logarithmic transformation of the data was performed (Barnes and Bagenal 1951; Oviatt and Nixon 1973). Transformed data approached a normal distribution. The significance of temporal and spatial differences in mean C/UE of each species was tested by single classification analysis of variance. Because of the smaller number of stations sampled in each statistical area in 1975, fewer significant differences in C/UE were obtained between areas and between seasons. However, the general trends observed in 1975 were identical to those of 1974 and support the view that the statistical differences observed in 1974 were the result of characteristic patterns of abundance of the six species in the lake. Analysis of temporal and spatial differences were performed on numerical and biomass data. Identical trends were evident in these analyses.

Stomach content analyses were performed on all monthly samples collected between June 1974 and May 1975. Diets of the fish collected in the north and central basins, which were similar in terms of species composition and levels of primary production, were compared with those of fish collected from Newport Bay (which was the most productive area of the lake and had the most diverse fish fauna). For each sampling period, 20 fish of each species collected in each of the two areas were examined for food content. Fork length (to the nearest millimetre) and weight (to the nearest centigram) was recorded for each fish sampled. The food was removed from the stomach (in the case of the Cyprinidae and Cyprinodontidae, which lack a true stomach, the portion of the gut anterior to the first intestinal loop was used) and weighed to the nearest 0.1 mg after the excess moisture had been removed. Gut contents were then spread uniformly on a microscope slide and examined. Prey items were identified at low magnification under a compound microscope using Edmondson et al. (1959) as a key. Frequency of occurrence (Hynes 1950) of each prey item was recorded. Because of the small size of the stomachs and the prey, and the poor condition of the prey items in the gut (minnows chew their food, Hynes 1950), precise volumetric determinations of the relative volume of the various food items in the gut was impossible. Instead the relative volume of each prey was ranked on a scale ranging from 1 to 10. This ranking was based on the number of prey in each group and a knowledge of the relative sizes of intact organisms. Diel-feeding periodicity of the species studied was determined by 24-h sampling of two stations located in the north basin and in Newport Bay during July and August 1974 and 1975. Collections were made every 3 h over the 24-h interval. Stomach analyses were performed on 20 fish of every species collected during each 3-h interval. Composition of the diet and degree of stomach fullness were assessed. Fullness indices C_R (expressed in percentage) were calculated for each fish using the formula:

$$C_R = \frac{\text{weight of food in stomach}}{\text{weight of fish}} \times 100 \text{ (Windell 1971)}$$

and mean values were calculated for each 3-h interval. Similarity in the diet of any two species was determined by calculating values of overlap in food utilization (Horn 1966). $C\lambda$ (percent overlap) was calculated as follows:

$$C\lambda = \frac{\Sigma p_{ik} \cdot p_{jk}}{\Sigma p_{ik}^2 + \Sigma p_{jk}^2}$$

where p_{ik} is the proportion of resource k utilized by species i. Identical diets give an overlap value of 1.00. This index has been commonly used to measure similarity in the diets of any two species (e.g. Holmes and Pitelka 1968; Zaret and Rand 1971) and the relationship between food overlap and interspecific competition has been discussed in detail elsewhere (Colwell and Futuyama 1971; Vandermeer 1972; Schoener 1974a; Sale 1974).

Results

Abundance and Biomass in Relation to the Production Gradient

Abundance and biomass of the six littoral zone species was higher in the more productive Newport Bay area than in any of the three other statistical areas. Biomass exhibited an orderly reduction toward the north end of the lake, apparently in response to the lowered production at other trophic levels (Fig. 2). Differences in the grouped geometric C/UE were significant for numbers ($F = 5.23$; df = 3, 244; $P < 0.001$) and biomass ($F = 3.07$; df = 3, 244; $P < 0.01$). The relative abundance and biomass of littoral zone fishes in the four statistical areas corresponded well with earlier findings for lower trophic levels and for the pelagic perch community (Dermott 1974; Ross and Kalff 1975; Nakashima and Leggett 1975). The ratio of biomass C/UE (all species combined) between Newport Bay and

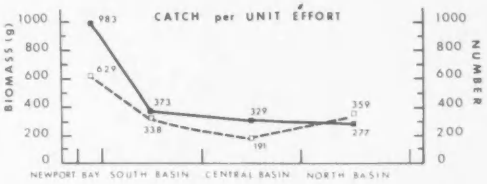

FIG. 2. Combined relative abundance (dashed line) and relative biomass (solid line) of six littoral zone species in the four statistical areas of Lake Memphremagog in 1974 and 1975.

south, central and north basins was 2.6:1, 3.0:1, and 3.5:1, respectively; for numbers C/UE the corresponding values were 1.9:1, 3.3:1, and 1.8:1. Differences between ratios of biomass and numbers C/UE resulted from differences in the average weight of the dominant species in the different basins, the mimic shiner (dominant in northern areas) weighing on average approximately 1 g and the silvery minnow (dominant in Newport Bay) weighing on average approximately 3.5 g. No statistical differences in numbers or biomasses were observed between statistical areas when analyzed on a monthly basis. However, examination of the monthly data for number and biomass indicated consistently higher values in Newport Bay than in any other sections (sign test, Siegel 1956; $P < 0.05$ all comparisons).

Distribution of Fish Species Along the Production Gradient

While the biomass and abundance of the littoral zone fish community of Lake Memphremagog was positively related to the nutrient and production gradients in the lake as a whole, the patterns of abundance of individual species were more varied. Three distinct groups were recognizable: (1) those reaching their maximum abundance in the area of maximum primary and secondary production (silvery minnow, golden shiner, johnny darter, and banded killifish); (2) those equally distributed along the gradient (bluntnose minnow); and (3) those most abundant in the northern end of the lake where production at lower trophic levels was minimum (mimic shiner).

The mimic shiner was the most abundant fish of the littoral zone in general and of the mesotrophic north and central basins of the lake in particular, accounting for 75.6 and 71.6% of the fishes collected in central and north basins, respectively, and 23.3 and 30.2% of the total numbers of the fishes collected in the south basin and Newport Bay, respectively. Between area differences in the geometric C/UE of the species were highly significant ($F = 9.30$; df = 3, 244; $P < 0.001$). On a monthly basis this species was also found to consistently occur in greatest abundance in the north and central basins.

The abundance of the bluntnose minnow was not affected by the production gradient. This species appeared regularly in small numbers at most of the stations in all basins, representing 3.9% of the fishes collected in Newport Bay and 7, 9.8, and 5.5% in the south, central, and north basins, respectively. The higher proportions recorded for northern sections resulted because fewer fish of all species were caught in these areas and not because of an absolute increase in abundance of the bluntnose minnow. Geometric C/UE of this species was not significantly different between basins ($F = 1.85$; df = 3, 244; $0.75 < P < 0.90$) either on a global or on a monthly basis.

The patterns of abundance of the johnny darter and of the golden shiner were very similar and closely paralleled the nutrient and production gradients. The geometric C/UE of both species was significantly higher in the southern regions (johnny darter: $F = 12.39$; df = 3, 244; $P < 0.001$; golden shiner: $F = 5.60$; df = 3, 244; $P < 0.001$). Monthly patterns for these species also revealed this tendency, although it was much more obvious for the johnny darter than for the golden shiner. This may occur because individuals of the latter species were generally very local in their distribution. As many as 2000 fishes were frequently taken in a single haul, while at other times very few were collected. This extreme concentration of members of this species at some locations may have rendered the logarithmic transformation less effective in normalizing the data, especially when the number of stations sampled was small. The golden shiners accounted for 11% of all fishes collected in the southern areas and 3% of all fishes collected in the north. In contrast, the johnny darter was distributed more evenly and occurred in small numbers at most of the sampling sites. They were somewhat less abundant than the golden shiner, forming 7 and 1.5% of the fishes collected in the southern and northern areas, respectively.

The patterns of abundance of the two remaining species considered, the banded killifish and the silvery minnow, were similar, being greatest in the south. However, their abundance decreased much faster toward the north. The banded killifish were almost exclusively limited to the Newport Bay area, being very scarce in the south basin, the few fish collected there being taken within 3 km of the northern limit of Newport Bay. Only two fish of this species were collected in the two northern statistical areas. The silvery minnow, which is the second most abundant fish in the littoral zone of Lake Memphremagog, constituted 37.3 and 42.8% of all fish collected in Newport Bay and the south basin, respectively, and only 3.4% of all fish collected in the central and north basins combined. Differences in C/UE between basins were highly significant ($F = 16.64$; df = 3, 244; $P < 0.001$).

During the course of the study, it became clear that the distribution of young-of-the-year (0+) silvery minnows was distinctly different from that

of the older fishes (1+). The two size-groups were therefore considered separately. Adult silvery minnows (1+) are obligate detritivores and were largely restricted to Newport Bay and the south basin. Differences in the geometric C/UE of 1+ fish between basins were highly significant ($F = 7.96$; df = 3, 244; $P < 0.001$). Important seasonal differences in the abundance of 1+ also occurred in Newport Bay ($F = 2.52$; df = 8, 61; $P < 0.05$). The greatest abundances occurred in the early summer (May–July) of both 1974 and 1975, which corresponds to the immediate postspawning period for species at this latitude (Raney 1939). Abundances were uniformly very low in the rest of the lake at this time and in the entire lake after August.

Young-of-the-year (0+) silvery minnows had a different and more complex distribution. They first appeared in the catches at approximately 33 mm fork length in mid-July. 0 year silvery minnows were most abundant in the southern statistical areas at all times and were totally absent from the July 1974 catches in the two northern areas. Their abundance in the northern areas increased as the summer progressed and in August no statistical differences occurred in the relative abundance between areas ($F = 1.21$; df = 3, 25; $0.50 < P < 0.75$). By October their abundance in the northern areas had declined sharply. This change was accompanied by a large increase in C/UE and in absolute numbers in the southern areas, the changes being most pronounced in 1974. The higher concentration of adults in the southern statistical area and the increase in numbers of 0+ fish in the northern areas over the summer suggests a dispersion of 0+ fish from the south basin into the northern areas at this time.

Food Habits

Food habit studies were used to determine the major sources of energy for each of the species occupying the highly productive Newport Bay area and the less productive central and north basins. In the analyses algae were grouped because they represented a negligible proportion of the diet of all species. The algae were mainly of the blue green (*Lyngbia* spp.) type. Organic detritus, which was found in abundance in the diet of some species, was composed of unidentifiable organic matter and fine sediment particles. No benthic organisms were found in abundance in the stomach containing sedimentary materials. The Cladocera was composed mainly of daphnids and *Bosmina* sp.; *Diptera* adults and larvae belonged almost exclusively to the family Chironomidae.

Food Habits and Resource Separation Among Fishes of the Central and North Basins

The diet of the mimic shiners occupying the north and central basins was quite specialized, being comprised mainly of flying insects (mostly small Diptera) in May, August, and September and cladocerans in July. Diptera larvae were consumed in large numbers only in June. This general pattern of feeding is typical for the species and has been reported previously by Black (1945) and Moyle (1973). The diet of the golden shiner was similar to that of the mimic shiner. The main food item was flying insects (mostly small Diptera), which were dominant in the stomach of the fishes collected in the northern areas throughout most of the study interval. Cladocerans and chironomid larvae were the other major food items. Cladocerans were important only in June when they were at their maximum abundance in the environment. Mayfly larvae were consumed in large numbers in May and October. In general the diet of the golden shiner, as observed in the samples from the north and central basins, is very similar to that previously reported for the species (Keast 1966; Keast and Webb 1966). Food overlap values between the mimic and golden shiners, on a monthly basis (Table 2), were high, being over 70% in 3 of 4 mo. However, these two species were separated by their habitat preferences, the mimic shiners reaching their maximum abundance on sandy-bottom habitat with minimum plant growth, while golden shiners were most abundant in areas having heavy macrophyte growth.

Bluntnose minnows occupying the northern areas utilized a broad variety of food items. Organic detritus was the main food source, especially in the late summer, but adult insects, mayfly nymphs, and cladoceran were eaten in important amounts. These findings agree with those of Kraatz (1928), Keast (1965), and Moyle (1973). The diet of the bluntnose minnow overlapped very little with that of the other littoral zone species occupying the northern areas. Only on one occasion (June) did relatively high overlap (62.9%) occur with another littoral zone species (golden shiner, Table 2).

The johnny darter is known to be a specialist predator of chironomid larvae (Turner 1921; Karr 1963; Balesic 1971; Lotrich 1973). Chironomid larvae constituted 48–75% of the volume of the stomach content of the species in the northern areas. Amphipods were important in the diet (40% by volume) only in September when they are at their maximum abundance in Lake Memphremagog (Dermott 1974). Cyclopoid copepods composed the balance of the diet of the

TABLE 2. Food overlap (percent) matrices for six littoral zone fishes of Lake Memphremagog.

North and Central Basins	Newport Bay						
	N. volucellus	N. crysoleucas	P. notatus	H. nuchalis 1+	H. nuchalis 0+	F. diaphanus	E. nigrum
June 1974							
N. volucellus		0.349	0.012	0.734	—	0.876	0.777
N. crysoleucas	0.397		0.353	0.604	—	0.045	0.055
P. notatus	0.502	0.629		0.006	—	0.028	0.016
H. nuchalis 1+	—	—	—		—	0.510	0.299
H. nuchalis 0+	—	—	—	—		—	—
F. diaphanus	—	—	—	—	—		0.921
E. nigrum	—	—	—	—	—	—	
July 1974							
N. volucellus		0.383	0.757	0.674	0.236	0.205	0.415
N. crysoleucas	0.182		0.261	0.152	0.102	0.128	0.692
P. notatus	0.808	0.012		0.980	0.000	0.141	0.163
H. nuchalis 1+	—	—	—		0.010	0.119	0.046
H. nuchalis 0+	—	—	—	—		0.004	0.027
F. diaphanus	—	—	—	—	—		0.396
E. nigrum	0.233	0.000	0.090	—	—	—	
August 1974							
N. volucellus		0.033	0.433	0.433	0.442	0.646	0.895
N. crysoleucas	0.940		0.028	0.028	0.030	0.042	0.024
P. notatus	0.123	0.061		1.000	0.999	0.701	0.540
H. nuchalis 1+	—	—	—		0.999	0.702	0.541
H. nuchalis 0+	0.413	0.222	0.612	—		0.718	0.555
F. diaphanus	—	—	—	—	—		0.894
E. nigrum	0.110	0.003	0.066	—	0.033	—	
September 1974							
N. volucellus		0.727	0.000	0.000	0.000	0.029	0.000
N. crysoleucas	0.781		0.015	0.014	0.019	0.034	0.012
P. notatus	0.006	0.262		1.000	0.997	0.072	0.116
H. nuchalis 1+	—	—	—		0.997	0.072	0.116
H. nuchalis 0+	0.023	0.265	0.984	—		0.075	0.121
F. diaphanus	—	—	—	—	—		0.983
E. nigrum	0.001	0.138	0.033	—	0.031	—	
May 1975							
N. volucellus		0.144	0.998	1.000	—	0.000	0.329
N. crysoleucas	0.792		0.156	0.145	—	0.716	0.648
P. notatus	0.467	0.585		0.998	—	0.019	0.340
H. nuchalis 1+	—	—	—		—	0.000	0.324
H. nuchalis 0+	—	—	—	—		—	—
F. diaphanus	—	—	—	—	—		0.271
E. nigrum	0.037	0.093	0.305	—	—	—	

species. Organic detritus and sediment particles were found in a constant proportion (approximately 20% by volume) throughout the study and may have resulted from accidental ingestions while feeding on prey of benthic origin. The diet of the johnny darter exhibited very low overlap with other littoral zone species of the northern areas (Table 2).

FOOD HABITS AND FOOD RESOURCE SEPARATION AMONG THE FISHES OF NEWPORT BAY

Food habits and patterns of resource utilization of the golden and mimic shiners and of the bluntnose minnow were very different in the more productive Newport Bay area. Flying insects (mainly chironomids) remained the dominant

food item in the diet but benthic food organisms were much more abundant in the diet than in fish from the northern areas. Larvae of chironomids, ephemeroptera, and odonata nymphs comprised 9–45% of the diet by volume. Cladocera were important (63% by volume) in June. The balance of the diet was comprised mainly of organic detritus. During May and July, when chironomid larvae were the major diet item, the diet of the golden shiner overlapped strongly with that of the johnny darter and the banded killifish (Table 2).

Mimic shiners resident in Newport Bay also relied more heavily on benthic food organisms than did their conspecifics in the northern areas. Flying insects, the dominant diet item in the north, were a minor item in Newport Bay, except in September, when they were the sole food item observed. The diet of the mimic shiner population of Newport Bay was composed of organic detritus and chironomid larvae. Chironomid larvae comprised 27–65% of the diet by volume from June to August and organic detritus constituted the balance. Some detritus may have been ingested accidentally as a result of feeding on chironomid larvae during June, July and August. However, in May it was the sole item in the diet. Because of these changes in the diet in Newport Bay, the diet of the mimic shiner commonly overlapped strongly with all the littoral zone species of Newport Bay (Table 2). High diet overlap occurred between the mimic shiner and the banded killifish and johnny darter as a result of their common exploitation of chironomid larvae as the major food item in June and August (Table 2). Their heavy reliance on detritus in May and July also resulted in extensive diet overlap with bluntnose and silvery minnows in those months (Table 2). The diets of the mimic shiner and golden shiner overlapped strongly only in September when both species relied heavily on flying insects (small Diptera).

The diet of the bluntnose minnow was more specialized in Newport Bay where organic detritus comprised 85–100% of the total stomach volume throughout the course of the study with the single exception of June 1974 when adult Diptera were eaten almost exclusivly. Moyle (1973) noted that bluntnose minnows are quick to utilize abundant temporary food sources such as emerging Diptera, and this may explain this sudden and dramatic shift in the diet of the species in Newport Bay. Generally, the composition of the diet of the Newport Bay population of bluntnose minnows agreed with the findings of Starrett (1950). Very high overlap in food utilization (>99%) occurred consistently between the bluntnose minnow and adult (1+) silvery minnows (Table 2).

The silvery minnow was the most specialized feeder of the six littoral zone species studied. Fish over approximately 40 mm fork length consumed organic detritus almost exclusively. Similar feeding patterns have been reported for the species by Flemer and Woolcott (1966). Other food items of significance occurred only in June when 46% of the volume was composed of cladocerans.

The diet of 0+ silvery minnows was very different from that of the adults. The fishes collected in Newport Bay in July 1974 (mean fork length = 32.7 mm; SD = 3.8 mm) had utilized cladocerans (mainly *Bosmina* spp.) almost exclusively (82% by volume) with the balance of the diet being composed of chironomid larvae (7%) and rotifers (8.4%). A month later, in August, the same fishes (mean fork length = 44.2 mm; SD = 5.6 mm) had shifted their diet almost exclusively to organic detritus (95% by volume) with only limited numbers of cladocerans (3% by volume) being taken. In contrast, those 0+ that had apparently dispersed into the north and central basins were significantly smaller than their conspecifics in the south in August (mean fork length = 39.4 mm, SD = 4.1 mm; $t = 7.80$, df = 237, $P < 0.01$) when the major portion of their diet was cladocerans (49% by volume) and flying insects (11% by volume). However organic deritus was becoming important in the diet (39% by volume) at that time. By October, the diet of 0+ silvery minnows in the northern areas had also shifted almost exclusively to organic detritus. Such changes in the diet of detritivorous fishes are not uncommon. Albertini-Berhaut (1974) has reported similar findings in the case of mullets (*Mugil* spp.). 0+ silvery minnows did not overlap strongly with any other littoral zone species while their diet was composed mainly of cladocerans.

Only the johnny darter showed no important differences in diet between the northern areas and Newport Bay. The food items consumed and the temporal changes in the diet were similar in the two areas. Chironomid larvae occurred in somewhat smaller quantities in the stomachs of fish resident in Newport Bay, while amphipods and cyclopoid copepods were used more intensively. In contrast to the situation in the northern areas, the diet of the johnny darter population of Newport Bay overlapped strongly with that of the other five species (Table 2). Overlap was intensive with the banded killifish (92, 89, and 98% in June, July, and August, respectively). Overlap in diet between these two species was reduced in May (21%) when johnny darters fed heavily on copepods (50% by volume) and in July when the killifish fed heavily on amphipods.

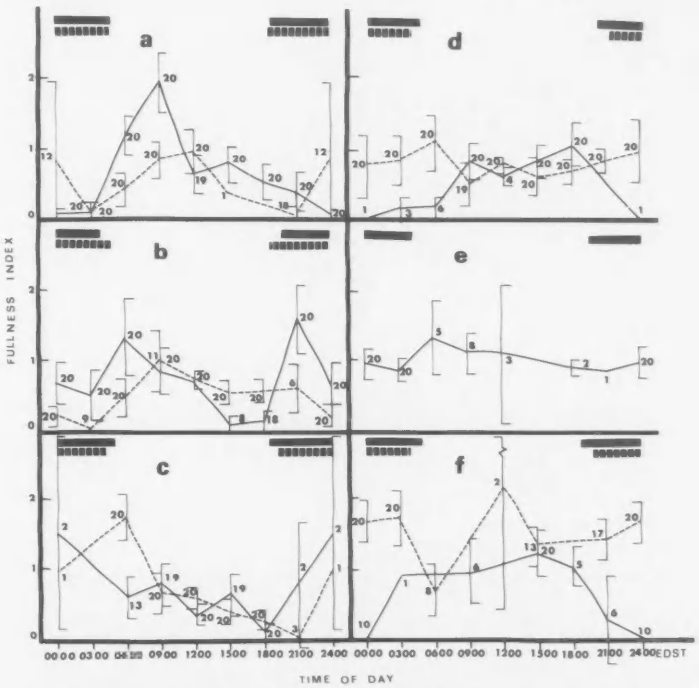

FIG. 3. Daily feeding periodicities (fullness index ±2 SE) of six littoral zone fish species of Lake Memphremagog. Dark bars indicate hours of darkness; numbers beside each point indicate the number of fish used in the calculation of the mean. *Left column*: crepuscular species. a, *Hybognathus nuchalis*: solid line, central basin, August 19, 1974; dotted line, Newport Bay, August 22, 1974. b, *Etheostoma nigrum*: solid line, Newport Bay, July 1, 1975; dotted line, Newport Bay, August 22, 1974. c, *Notropis volucellus*: solid line, central basin, August 19, 1974; dotted line, Newport Bay, July 23, 1974. *Right column*: diurnal species. d, *Pimephales notatus*: solid line, central basin, August 19, 1974; dotted line, Newport Bay, July 1, 1975. e, *Fundulus diaphanus*: Newport Bay, July 4, 1975. f, *Notemigonus crysoleucas*: solid line, central basin, August 19, 1974; dotted line, Newport Bay, July 1, 1975.

The banded killifish, which was absent in the northern statistical areas, had the most diverse diet of any of the six littoral zone species in the southern areas. Chironomid larvae, amphipods, and organic detritus were the main components of the diet. These results agree with the findings of Smith (1947). The banded killifish was the only species of the littoral zone that utilized important quantities of ostracods, especially in late summer. This was also noted by Keast (1965) in his study of the fishes of Lake Opinicon. Chironomid larvae were eaten in abundance in early summer, while amphipods were eaten in abundance only after the month of July. Organic detritus may have been ingested accidentally with the other foods of benthic origin.

FEEDING PERIODICITIES AND TEMPORAL SEPARATION IN FOOD UTILIZATION

Diel periodicity in the food uptake of the six littoral species studied was used to determine whether species with overlapping diets were separated in the temporal dimension. Three species were found to be crepuscular in their habits (silvery minnow, johnny darter and mimic shiner) (Fig. 3a, b, c) and two were diurnal (bluntnose minnow and golden shiner) (Fig. 3d, f). Emery (1973) reported that Cyprinidae and Etheostomatinae were generally diurnal in their activity. Most of the feeding apparently occurs between sunrise and sunset, although some exceptions may occur. On three occasions some fish were found

to feed at night (bluntnose minnow, banded killifish, and golden shiner) (Fig. 3d, e, f), which differs from earlier reports by Keast and Welsh (1968). No evidence of significant temporal separation in feeding activity was observed between species exhibiting high overlap in diet.

Discussion

Lake Memphremagog exhibits a distinct production gradient along its long axis with the highest levels of primary and secondary production occurring in its southern regions. The composition and pattern of resource utilization of the permanent littoral zone fish community of the lake differed along its length in apparent response to this gradient. Species diversity (Nakashima et al. 1977), relative abundance, and biomass were highest in the more productive southern areas in a pattern similar to that observed in stream ecosystems (Sheldon 1968; Lotrich 1973; Small 1975). In addition, much greater overlap was observed in the diets of species inhabiting the southern areas, and species feeding exclusively on organic detritus were largely restricted to Newport Bay and the south basin. The average ratio of numbers and biomass of fish in the littoral zone of the southern and northern areas of Lake Memphremagog was 2.5:1 and 3:1, respectively. This was very similar to biomass and production ratios determined for the other trophic levels of the lake (algae:biomass 1.6:1, production 1.25:1, Ross and Kalff 1975; benthic invertebrates:biomass 3:1, Dermott 1974; and perch:biomass 2.5:1, Nakashima and Leggett 1975). The S:N biomass ratio in Lake Memphremagog thus appears relatively constant for all trophic levels and follows the general patterns exhibited in the nutrient gradient (Kalff and Leggett 1976). This suggests that higher numbers and biomass of littoral zone species in the southern areas of Lake Memphremagog occur in direct response to the greater food availability there.

The composition of the littoral zone fish community and the pattern of utilization of the available resources in the lake also appear to be strongly influenced by differences in primary and secondary production (food availability) along its length. Patterns of food utilization by individual species were significantly different at the different levels of food abundance. Three of four populations occurring in Newport Bay and in the northern areas exhibited marked differences in the pattern of their food utilization (χ^2, $P < 0.01$) in all but two of 19 possible comparisons. The feeding niche of the mimic and golden shiners and of the bluntnose minnows showed marked differences between areas. The major shift in the diet of these three species resulted from an important increase in the proportion of food of benthic origin in the south, accompanied by a parallel reduction in the numbers of surface and planktonic organisms. The greater abundance of benthic food items in general, and of the larave of Chironomidae in particular, in the diets of the mimic and golden shiners was unexpected because these items were already heavily preyed upon in the south basin and Newport Bay areas by the banded killifish and the johnny darter. Dermott (1974) showed that the standing crop of Chironomidae was 3 times higher in the more productive southern areas. This ratio was very similar to the ratio of abundances of littoral zone fish species in the two areas. However, approximately 40% of the littoral zone fish biomass in the south was comprised of silvery minnows, the only species of the six that does not feed on benthic invertebrates. This suggests that a more abundant chironomid food resource exists in the southern areas, relative to the northern, for the five remaining littoral zone species found to actively utilize benthic food items. Werner and Hall (1976) reported that when competitive pressure was released, sunfish (*Lepomis* spp.) concentrated their feeding on prey items having higher energy content. A similar response appears to be operating in Lake Memphremagog, where zooplankton and emerging and terrestrial insects, the dominant food items of the less productive northern areas, are abandoned in favor of the more abundant chironomid larvae and other benthic food items.

Only minor changes were observed in the diet of the johnny darter in relation to the production gradient. In this species, the diet was more diverse in the more productive south basin. However, the diet was quite similar between areas and did not differ significantly from previous findings for the species (Turner 1921; Karr 1963; Lotrich 1973). These results were not unexpected since the johnny darter is known to be very restricted in its choice of food items (Lotrich 1973).

The changing patterns of food utilization observed among the littoral zone fish species of Lake Memphremagog in response to the production gradient are consistent with, and predicted by, the results of earlier workers who studied patterns of food utilization in response to seasonal changes in food availability. Nilsson (1960, 1967) and Zaret and Rand (1971) observed that in periods of low food abundance, food niches became narrower, with individual species concentrating more exclusively on few specific food items. This resulted in reduced overlap in food utilization between species in times of food

shortage. Greater specialization in individual diet and reduced food overlap values are characteristic of the feeding ecology of littoral zone species of the less productive northern areas of Lake Memphremagog. In the northern areas high food overlap values were uncommon. In contrast, in the more productive southern areas, high overlap values were common. The reduction in overlap in northern areas was achieved by (1) exploiting food items little used by the littoral zone species of the more productive Newport Bay area and (2) a reduction in the number of littoral zone species occupying the area.

The high food overlap observed in the southern areas apparently resulted from the opportunistic use of the more abundant benthic invertebrates, which results, in turn, from markedly higher production at other trophic levels. Organic detritus formed a significant component of the diet of all littoral zone species in Newport Bay, with the exception of the johnny darter. Two of these species (bluntnose and silvery minnow) used detritus as their sole energy source and their numbers were greatly reduced in the northern areas where sedimentation rates are lower (G. Spiller, McGill University, personal communication). This allowed an extensive overlap in diet between species utilizing organic detritus for food in the Newport Bay area, whereas organic detritus was a limiting resource in the central and north basins. This was suggested by the important shift in the diet of the bluntnose minnow population inhabiting the northern areas, which complements its utilization of detritus with animal prey items and by the scarcity of the stenophageous silvery minnow. The silvery minnow appears unable to maintain a significant permanent population in the northern areas, although 0 yr fish of this species, being planktivorous, do disperse into the northern area. However, their numbers were observed to decline in the north at the time when their diet changed from planktonic invertebrates to organic detritus.

An alternative possibility concerning the restriction of 1+ silvery minnows to the Newport Bay and south basin areas is that morphometric differences between the basins (north and central basins being deeper than Newport Bay) make benthic food items inaccessible to the species in the northern areas. This hypothesis was discounted because the morphometry of the south basin is very similar to that of Newport Bay, and yet the abundance of silvery minnows declines sharply in the south basin. This decline parallels the sharp decline in nutrient levels in this area.

Interspecific competition for food appeared to play a limited role in the distribution of the littoral zone fish species along the nutrient/production gradient of Lake Memphremagog. However, it played a major role in creating the food shifts between populations occupying the productive Newport Bay area and the less productive northern areas. The various mechanisms of "interactive segregation" (Nilsson 1967), which facilitate reduced competition and allow species to coexist, have been reviewed by Schoener (1974a), who concluded that habitat, food, and temporal patterns of activity were the three principal means by which ecological segregation of species was achieved. Schoener (1974a) considered habitat differences to be the most common means of species segregation. However, this was not observed in Lake Memphremagog. In Lake Memphremagog the principal mechanism of ecological segregation between the littoral zone fish species appears to be differences in the food consumed, as it is in most freshwater fish communities (Keast 1965, 1966; Hartley 1948; Starrett 1950; Maitland 1965; Gee and Northcote 1963; Keast and Webb 1966; Gibbons and Gee 1972; Moyle 1973; Mendelson 1975). Competition for food appears to be less intense in the productive southern areas of the lake. This is suggested by the high food overlap values (Vandermeer 1972; Schoener 1974b; Sale 1974).

In the north, competition for food resources is more intense and plays a greater role in determining patterns of resource utilization. This is evident from the low food overlap between species and in the pronounced shifts in diet. Reductions in the abundance of benthic food items (principally chironomids) associated with reduced primary production and algal sedimentation result, in turn, in shifts in the food niche of the golden and mimic shiners from the benthic diet of the south to a more pelagic diet, the benthic resource being used almost exclusively by the johnny darter whose diet is very similar in the northern and southern areas. The banded killifish appears to be the only species excluded from the northern areas through competition for the available food resources. A small population of killifish coexists with other benthic feeders in Newport Bay, where the benthos appears to be a nonlimiting resource. However, no killifish population was found in northern areas, where competition for the same resources seems more intense. The low relative abundance of silvery minnow adults in the northern areas appears to result primarily from the reduced availability of benthic detritus there rather than from competition from other species for this resource.

These findings lead us to conclude that the differences in the levels of primary and secondary

production (food availability) along the axis of Lake Memphremagog, resulting from the presence of a pronounced nutrient gradient, are the principal causes of observed changes in the species diversity (Nakashima et al. 1977), community composition, relative biomass, and patterns of resource utilization in the littoral zone fish community of the lake.

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A Leukocytolytic Factor Isolated from Cultures of *Aeromonas salmonicida*[1]

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Fuller, D. W., K. S. Pilcher, and J. L. Fryer. 1977. A leukocytolytic factor isolated from cultures of *Aeromonas salmonicida*. J. Fish. Res. Board Can. 34: 1118–1125.

A substance characterized as a glycoprotein, isolated from the supernatant fluids of broth cultures of *Aeromonas salmonicida* by a combination of ammonium sulfate and ethanol precipitations followed by chromatography on DEAE-cellulose, was cytolytic for rainbow trout (*Salmo gairdneri*) leukocytes, and antigenic when injected into rabbits. The ratio of protein to hexose determined by analysis of the purified fraction was between 0.35 and 0.45, and small amounts of amino sugars were detected. A virulent strain of *A. salmonicida* produced much more of this factor than an avirulent strain. This factor was cytolytic for leukocytes in vitro and also produced a pronounced leukopenia when injected intravenously in adult rainbow trout. When injected in small coho salmon (*Oncorhyncus kisutch*) 8–13 cm long together with about one LD50 of live *A. salmonicida* 36 of 40 fish succumbed to the combination, whereas only 14 of 40 died from an injection of the bacterium alone. Thus, the pathogenicity of the organism was enhanced, presumably by increasing the susceptibility of the host. Hence, this glycoprotein apparently is one of the virulence factors of this bacterium.

Key words: leukocytolytic factor, *Aeromonas salmonicida*, glycoprotein, virulence factor

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Une substance ayant les caractéristiques d'une glycoprotéine, isolée des liquides surnageants de cultures dans un bouillon d'*Aeuromonas salmonicida* par une combinaison de précipitations par sulfate d'ammoniac et éthanol suivies de chromatographie sur cellulose-DEAE, a un effet cytolytique sur les leukocytes de la truite arc-en-ciel (*Salmo gairdneri*) et un effet antigénique lorsque injectée dans des lapins. Le rapport protéine/hexose déterminé par analyse de la fraction purifiée se situe entre 0.35 et 0.45, et on détecte une faible quantité d'amino-sucres. Une lignée virulente d'*A. salmonicida* produit ce facteur en quantité beaucoup plus forte qu'une lignée non virulente. Ce facteur a une action cytolytique sur les leukocytes in vitro, en plus de produire une leukopénie prononcée quand des truites arc-en-ciel en reçoivent par voie intraveineuse. Quand on injecte ce facteur à de jeunes saumons coho (*Oncorhynchus kisutch*) de 8 à 13 cm de longueur, en même temps qu'environ une DL50 d'*A. salmonicida* vivants, 36 sur 40 poissons succombent à la combinaison, alors que seulement 14 sur 40 meurent à la suite d'une injection de la bactérie seule. Le pouvoir pathogène de l'organisme est donc rehaussé, probablement par une susceptibilité accrue de l'hôte. Cette glycoprotéine, semble-t-il, serait un des facteurs de virulence de cette bactérie.

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The possibility that *Aeromonas salmonicida*, the causative agent of furunculosis in fish, may produce a leukocytolytic factor has been suggested by Bullock and McLaughlin (1970), Griffin (1954), Klontz et al. (1966), Mackie and Menzies (1938), and Mawdesley-Thomas (1969). However, the biochemical nature of such a factor has not, to our knowledge, been reported.

The work reported here was undertaken in an effort to determine whether a single fraction or product of this organism possessing cytolytic activity against leukocytes of salmonid fish could be detected, chemically characterized, and isolated in purified form. Chemical and immunological data resulting from this work indicate that the leukocytolytic factor isolated from cultures of *A. salmonicida* is glycoprotein in nature. Thus, it is distinct from the endotoxin, a lipopolysaccharide, which has been extracted from the cells and studied by Ross (1966), Anderson (1973), and Paterson and Fryer (1974).

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Materials and Methods

Bacteria

Two strains of *Aeromonas salmonicida*, both isolated from chinook salmon (*Oncorhynchus tshawytscha*) were used. The virulent strain was determined to have an LD50 at 20°C of approximately 10^2 cells for 2.5–8.6-g rainbow trout (*Salmo gairdneri*) and the avirulent strain an LD50 of approximately 10^8 cells. The LD50 was estimated by the method of moving averages (Meynell and Meynell 1965). All cultures were brought out of lyophilized stock, grown in brain heart infusion broth (BHI) (Difco) at 18°C for 48 h, then transferred to furunculosis broth (Difco). These two strains were compared with respect to the amounts of the leukocytolic factor produced by each.

Fish

Yearling rainbow trout used to supply leukocytes were maintained in 1-m circular tanks supplied with 12.2°C flowing, fish-pathogen-free well water. Juvenile coho salmon (*O. kisutch*) 8–13 cm in length were held in 68-ℓ fiberglass tanks supplied with flowing, fish-pathogen-free well water at 20°C during experiments.

Purification of Leukocytolytic Factor

Five millilitres of a 48-h BHI broth culture of *A. salmonicida* were introduced into 1-ℓ of furunculosis broth. This was incubated at room temperature with agitation for 72–96 h. Cells were then removed by centrifugation at 8000 × *g* for 20 min. Table 1 outlines the isolation and purification procedure from this point.

After learning that the leukocytolytic activity was eluted as a single peak between the 0.1 and 0.3 M NaCl concentrations, batch-fractionating techniques were utilized. DEAE Sephadex (Pharmacia Fine Chemicals, Piscataway, New Jersey) swollen in 0.3 M NaCl (1 g/50 ml) was mixed with the crude preparation (step 7 in Table 1). After equilibrating several hours the supernatant was separated from the gel by filtration through Whatman No. 1 filter paper and saved. The material was concentrated by precipitating with 3 vol of 95% ethanol, dissolving in distilled H_2O, then washing and concentrating on the XM-100A Diaflo membrane. The final product was stored at −20°C if not used immediately. This was the purified Fraction 1 (or LCL).

Protein was assayed by the Lowry method, using bovine serum albumin as standard (Williams and Chase 1968). The hexose content was determined by the anthrone method described by Chaykin (1966). Hexosamine concentration was assayed using Dische and Borenfreund's method (1950). Lipids were extracted using Folch et al.'s method (1957) with some modifications: (1) Five-tenths millilitre of sample was vigorously shaken with 9.5 ml of a 2:1 chloroform–methanol mixture for 5 min, then held at room temperature for 30 min. (2) Two millilitres distilled water were added to the tube and mixed. (3) The tube was centrifuged at 750 × *g* for 5 min and the upper phase removed and discarded. (4) The walls of the tube were gently rinsed with 1.5 ml of a solvent mixture (chloroform, methanol, and water, 3:48:47, respectively, by volume), which was then carefully removed by suction. (5) The pellet was mixed with 10.0 ml of methanol, then with 2 ml distilled water. (6) Steps 3 through 5 were repeated twice. One millilitre of this preparation was evaporated to dryness at 37°C and assayed for "free" lipids by Bragdon's method (1951). Bound lipids were extracted by first hydrolyzing 0.5 ml of sample with 1.0 ml 6 N HCl in a boiling water bath for 3 h. The mixture was neutralized with 6 N NaOH, then extracted and assayed for lipids by Bragdon's method (1951).

Table 1. Purification procedure used for fractionating LCL from culture supernatants.

1.	Culture supernatant freed from cells
2.	Add $(NH_4)_2SO_4$ to 0.8 saturation; discard supernatant
3.	Dissolve ppt. in H_2O; dialyze against H_2O 16 h; add Na acetate to a 5% concnt
4.	Add 5 vol ETOH; discard supernatant; dissolve ppt. in H_2O and bring Na acetate again to 5%
5.	Add 3 vol ETOH; discard supernatant; dissolve ppt. in H_2O and add 0.1 vol of a 5:1 chloroform *n*-butanol mixture and discard ppt.
6.	Bring supernatant to 5% Na acetate concn and add 3 vol ETOH
7.	Dissolve ppt. in H_2O, wash, and concentrate on an XM-100A Diaflow membrane; this concentrate is the crude prepn of the LCL factor
8.	Add NaCl to the concentrate to give a 0.1 M concn
9.	Apply to a DEAE-cellulose column and elute with a NaCl concn gradient from 0.1 to 2.0 M
10.	Collect fractions of eluate; fractions containing 0.1–0.3 M NaCl will contain the purified LCL

Serology

A New Zealand White rabbit was injected subcutaneously with an emulsion consisting of 1.0 ml (0.43 mg hexose) purified LCL factor and 1.0 ml Freund's complete adjuvant. A boster injection of 0.1 ml (0.26 mg hexose) LCL factor in saline was given intravenously 33 days later. About 25 ml blood was taken from the marginal ear vein 15 days after the booster injection. The serum was tested for precipitating antibodies by ring precipitation tests, filter sterilized, stored at −20°C, and was designated rabbit anti-Fraction 1 serum. This serum was used in macroscopic slide agglutination, ring precipitin, and Ouchterlony gel diffusion tests. The gel diffusion plates were prepared according to Carpenter (1965) with 15 ml gel/plate, and wells were cut with a 7-mm cork borer. The bottom of each well was sealed with a drop of molten gel.

Electrophoresis

The LCL factor was subjected to electrophoresis

using a 7% polyacrylamide gel (Davis 1964) in a slab-gel electrophoresis unit at 50 mA for 110 min (Anderson 1971). The gel was sliced into strips, stained for protein with Coomasie Brilliant Blue (Chrambach et al. 1967), and stained for carbohydrate using a modification of the Schiff-Nadi method (Williams and Chase, 1968). The gels were treated with 1% periodic acid in 0.2 M sodium acetate for 30 min, then rinsed in running tap water for 1 h. They were then stained until completely dark (30–60 min) in a solution of equal volumes of 0.01 M α-naphthol in 10^{-4} M neutralized EDTA and 0.01 M *p*-phenylenediamine in 10^{-4} M neutralized EDTA plus ⅓ vol 3% H_2O_2, all mixed just before using. The gels were decolorized in 2–5% acetic acid until the red carbohydrate bands were visible, then rinsed in distilled H_2O.

LCL Factor Assay

Leukocytes were prepared by drawing blood from the fish by cardiac puncture into heparin (0.2 U/ml blood), mixing, and immediately applying 0.1-ml aliquots to acid-cleaned coverslips which were held in humidified chambers for 30 min. The coverslips were then gently rinsed with Hank's Balanced Salt Solution (HBSS) to remove erythrocytes and plasma and placed in small staining jars containing HBSS for maintenance. At 10-min intervals, to allow time for inspection at the end of the incubation period, two coverslips were removed from the maintenance medium and placed in small plastic petri dishes. Each coverslip had 0.4–0.5 ml test material in HBSS applied to it. The covered petri dishes were then placed in humidified chambers and incubated for 20 min at 18°C. At the end of the incubation period the coverslips were gently rinsed with HBSS, mounted wet on clean microscope slides, and examined by phase-contrast microscopy for leukocyte integrity and viability. Coverslip preparations exposed only to HBSS were also incubated for the duration of the test and examined as controls.

Damage to the leukocytes by the LCL factor was evidenced by morphological changes in the cells. There was a rapid loss of motility and cytoplasmic streaming, the pseudopodia were withdrawn, and the cells became rounded. The nuclei became very dense and highly refractile. The cells ultimately detached or disintegrated leaving remnants of membrane or other cellular debris on the glass. The process was easily followed microscopically and occurred in minutes after exposure to the LCL factor. The method was quantitative, and 1 leukocytolytic U/ml (1 LCL U) was defined as the lowest concentration of hexose per millilitre that caused visible leukocyte damage in 20 min at 18°C. In terms of the purified LCL factor a solution containing 1 LCL U/ml was found to be a solution containing 12.5 μg hexose/ml.

Determination of Normal Range of Leukocyte Counts in Adult Rainbow Trout

Thirteen adult rainbow trout weighing from 1.8 to 2.0 kg were selected for in vivo experiments with the LCL factor. It was necessary to determine the normal range of variation of the total leukocyte counts in these animals. For each count 0.2 ml of blood was taken from the caudal vessel and mixed with 0.05 ml of sodium heparin containing 20 U/ml. Two counts were made on each fish at 5-day intervals. They fell within the range of 17,000–49,000 cells/mm³ in all 13 fish. The mean of all 26 counts was 31,000.

Results and Discussion

Purification of the LCL Factor

When the crude preparation was applied to a DEAE-cellulose column three peaks were observed in the elution curve (Fig. 1). Of the three peaks only the first (Fraction 1) exhibited any activity against fish leukocytes. The protein to hexose ratio of this peak was approximately 0.4. This ratio for the succeeding peaks increased to approximately 0.7 for Fraction 2 and 7.6 for Fraction 3. The ratio for the LCL factor (Fraction 1) varied between 0.35 and 0.45 in different preparations. Analysis of a representative sample of the purified factor gave the following results: protein 0.32 mg/ml; hexose 0.73 mg/ml; hexosamine 0.01 mg/ml; and no free lipid or bound lipid.

The elution curve indicated that the active fraction was eluted from the column before the 0.3 M NaCl concentration was reached (Fig. 1), so batch fractionating with DEAE Sephadex in 0.3 M NaCl was initiated. Application of the product to a DEAE-cellulose column followed by elution produced a single peak.

Manipulation of pH and ultrafiltration methods failed to yield an active material that would pass the XM-100A Diaflo membrane. The fact that activity would however pass the XM-300 mem-

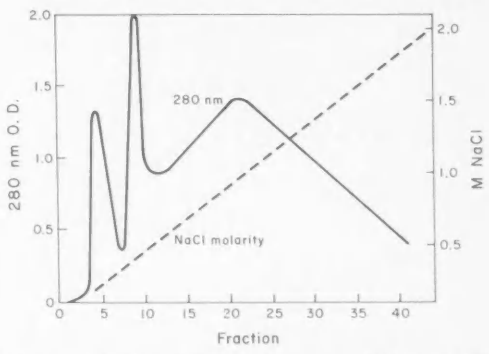


Fig. 1. Elution of the crude, or partially purified preparation of the LCL factor from a DEAE-cellulose column. The eluant was a linear NaCl concentration gradient from 0.1 to 2.0 M.

brane suggests a molecular weight between 100,000 and 300,000. The degree of purity achieved by the method described is indicated by both the electrophoretic analysis and the immunodiffusion data, which are described below.

Electrophoretic analysis of Fraction 1 (LCL) in the 7% polyacrylamide gel showed one very strong band of protein occupying the same position as a carbohydrate band on a parallel slice of gel. Both were located 18 mm into the small pore gel (Fig. 2). It also had a very faint second protein band at 29 mm with no matching carbohydrate. The latter band coincided with a strong protein band on the gel containing Fraction 2, which was probably due to contamination by the leading edge of Fraction 2 with Fraction 1 as it was eluted from the DEAE column. Fraction 2 separated into six protein bands. The one at 14 mm had a coincident carbohydrate band, but this was not seen with any of the other five. In Fraction 3 there was one protein band and an associated carbohydrate band at 4 mm. Thus, this method of analysis revealed that the LCL factor had only one major component, composed of protein associated closely with carbohydrate, with only a very small amount of a second protein with a different rate of migration in the column. All attempts to separate the protein and carbohydrate resulted in loss of activity and led to the conclusion that LCL is a glycoprotein.

Results of immunodiffusion tests relating to the purity of Fraction 1 (LCL) are shown in the photographs of Fig. 3. In Fig. 3 (*upper*) anti-Fraction 1 serum is in the center well and purified Fraction 1 in the left-hand well. A strong band of antigen antibody precipitate has formed between these wells, but there is no indication of the presence of a second component. There is also a faint but definite reaction between the anti-Fraction 1 serum and the purified *A. salmonicida* cell wall fraction in the top well, indicating that there is some of the LCL factor associated with the cell walls.

In Fig. 3 (*lower*) anti-Fraction 1 serum is in the center well and again has formed a single band with the purified Fraction 1 in the lower right-hand well and in the upper left-hand well. The two wells labeled T in Fig. 3 (*lower*) each contain antiserum against the whole cells of *A. salmonicida*. The serum at the upper right was prepared in rabbits, while that at the lower left in rainbow trout. Both had been absorbed with an excess of *A. salmonicida* endotoxin to remove any antibody against this component. However, each of them reacted with the purified LCL factor, giving bands that coalesced with those produced by the mono-specific anti-LCL serum. They

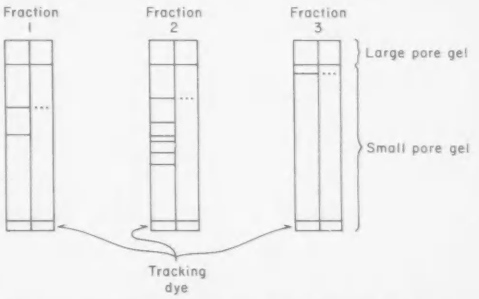


FIG. 2. Diagrams of polyacrylamide gels after electrophoresis of the three fractions representing the three peaks from the DEAE-cellulose column. Stained for protein with Coomasie Brilliant Blue and for carbohydrate by the Schiff-Nadi method.

both failed to react with the endotoxin in wells A and C because the antibody specific for that substance had been removed. Likewise, the anti-LCL serum failed to react with endotoxin, further confirming the separate identities of these two components. Combined results of the electrophoretic analysis and immunodiffusion tests indicate that a reasonably high degree of purification has been achieved.

COMPARISON OF LCL FACTOR FROM VIRULENT AND AVIRULENT STRAINS

Both the virulent and avirulent strains of *A. salmonicida* studied produced the leukocytolytic factor, but in different amounts. The amount of material obtained from the two cultures by precipitation procedures (before DEAE fractionation) was approximately the same. When these crude preparations were assayed for leukocytolytic activity it was found that about 10 times more of the avirulent preparation (1.9×10^{-2} mg hexose/ml) than of the virulent preparation (1.8×10^{-3} mg hexose/ml) was required to give a reaction with the fish leukocytes. However, after further purification by DEAE chromatography the concentration required to give solutions containing 1 LCL U/ml were about the same, i.e. 12.5 μg hexose/ml. This was true for the virulent and the avirulent preparations. However, immunodiffusion tests with anti-Fraction 1 serum indicated that the purified factors from both cultures gave identical, single-band reactions and were thus apparently identical. The only apparent difference between the active fraction produced by the virulent and avirulent culture was quantitative.

COMPARISON OF LEUKOCYTOLYTIC FACTOR AND ENDOTOXIN

Aeromonas salmonicida produces an endotoxin

and this material has been purified and studied in some detail by Paterson and Fryer (1974). The question arises as to whether this substance might be a leukocytolytic factor produced by this bacteria.

Experiments were undertaken to determine whether the LCL factor could be easily differentiated from the endotoxin. A litre of furunculosis broth culture of *A. salmonicida* was incubated at room temperature with aeration for 48 h. The cells were removed by centrifugation, and LCL was isolated from the supernatant by the method previously described. Endotoxin was extracted from the cells using trichloracetic acid (Paterson and Fryer 1974). When mice were injected with 4 mg of endotoxin to verify its toxic activity, all of them died, while controls receiving equal volumes of saline survived. Using the LCL assay method described earlier, no concentration of endotoxin up to 0.5 mg/ml exhibited any visible activity against the fish leukocytes. However, the LCL factor damaged or destroyed leukocytes at all concentrations from 0.1 to 0.25 mg hexose/ml. When tested by gel diffusion against anti-Fraction 1 serum there were no bands of precipitate between the endotoxin and the serum (Fig. 3, *lower*). Fraction 1, however, reacted with its specific antiserum and with anti-whole cell *A. salmonicida* serum, giving in each case single arcs of precipitate. These experiments indicate that the endotoxin does not have leukocytolytic activity and that it does not cross react with antisera against the LCL factor. Thus, these substances appear to be separate and distinct.

In Vivo Leukocytolytic Activity of LCL

It was of interest to determine whether LCL might have leukocytolytic activity in vivo in rainbow trout. After establishing the range of normal leukocyte counts in 13 trout weighing from 1.8 to 2.0 kg, as previously described, 8 of the fish were injected intravenously (i.v.) with 1.13 mg of Fraction 1 (measured as hexose), and 5 received a similar volume of saline alone. Total leukocyte counts were then made at intervals, beginning 5 h after injection and continuing for 120 h.

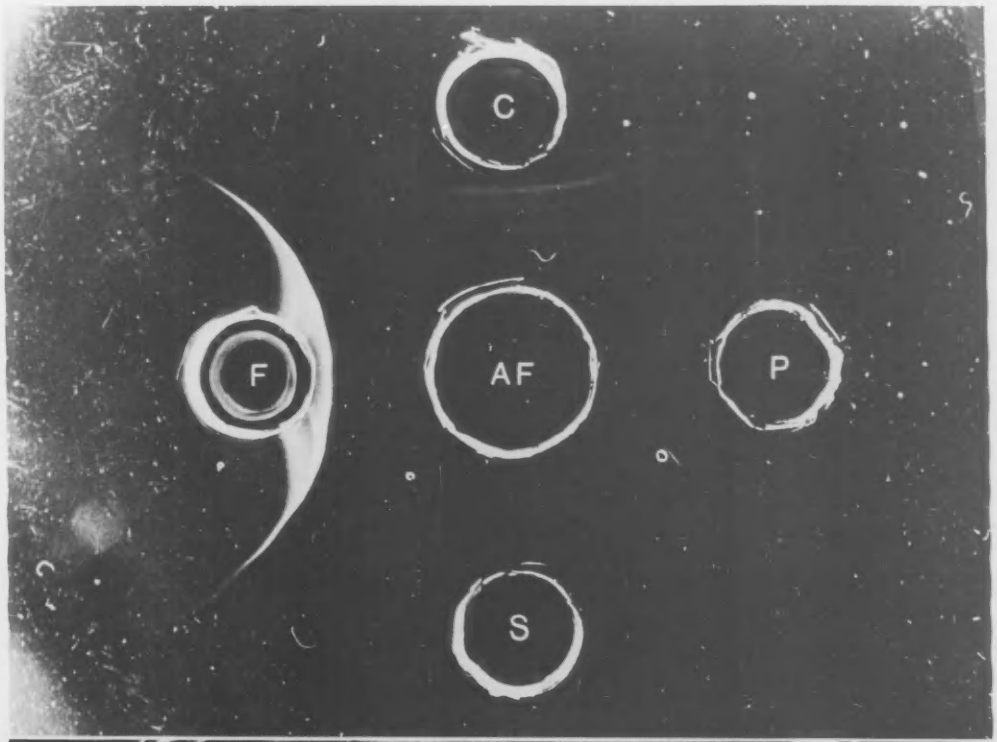
The results of these cell counts after injection are shown in Table 2. Within 5 h a distinct leucopenia had developed in all fish receiving Fraction 1, while those injected with saline still had counts in the normal range. Leucopenia was still present after 24 h, but by 48 h counts were again in the normal range. At the 72-h interval a slight leucocytosis appears to have developed, which is not evident in the saline controls. At 120 h all fish injected with Fraction 1 had normal cell counts. This experiment indicates that the LCL factor is indeed active when injected in the blood stream of rainbow trout, and capable of causing a leucopenia which may persist for at least 24 h.

Increase of Host Susceptibility to *A. Salmonicida* by the LCL Factor

The demonstration of the leukopenic effect of LCL when injected i.v. in rainbow trout suggested the importance of determining whether the injection of this factor could enhance the pathogenic effect or increase the percent mortality in fish infected with a minimal dose (about one LD50) of the bacterium. Accordingly, 160 healthy coho salmon 8–13 cm in length were divided into eight experimental groups of 20 fish each and maintained in pathogen-free water at 20°C. Two of these groups received parental injections of HBSS alone in a volume of 0.2 ml. Another two groups received the same volume of HBSS containing 0.04 mg of LCL expressed as hexose. Two other experimental groups received the same amount of HBSS containing about one LD50 of the virulent *A. salmonicida*, strain AS-SS-70. The remaining two groups received the 0.04 mg of LCL together with the same minimal dose of the bacterium. All fish were observed over a period of 10 days; dead fish were collected daily, autopsied, and cultures made from fragments of kidney tissue on BHI agar.

Results of the experiment (Table 3) showed that none of the fish injected with HBSS or with LCL alone died during the experiment or showed any indication of *A. salmonicida* at autopsy. Among the two groups receiving bacteria only, 8 of the 20 died in one case, and 6 of 20 in the other. *Aeromonas salmonicida* was isolated from all the dead fish and was not recovered from any of the sacrificed survivors. In the case of the two groups that received both LCL and bacteria, 18 of the 20 died in each group, and the bacterium

FIG. 3. (*Upper*) Immunodiffusion reactions with anti-Fraction 1 serum (anti-LCL). Antiserum in center well. F is purified LCL; C is purified *Aeromonas salmonicida* cell walls; P is protein precipitate from isolation procedure; S is an acid extracted polysaccharide from *A. salmonicida* cells. (*Lower*) Immunodiffusion reactions distinguishing purified LCL from endotoxin. Center well B contains anti-Fraction 1 (LCL) serum. T at top right contains anti-whole *A. salmonicida* cell serum prepared in rabbits, while T at lower left contains similar whole cell antiserum prepared in rainbow trout (*Salmo gairdneri*); in both cases these sera had been absorbed with an excess of *A. salmonicida* endotoxin. Wells labeled F contain purified LCL factor, and wells A and C contain *A. salmonicida* endotoxin.


C
F
AF
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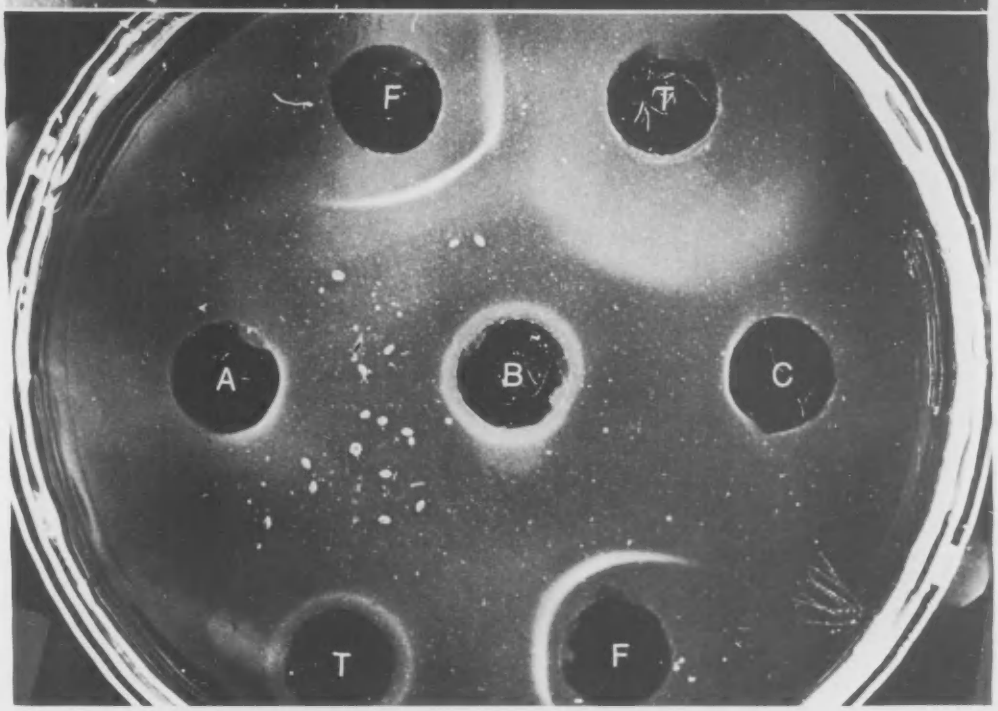
F
A
B
C
T
F

TABLE 2. Total white cell counts of nonimmunized 1.8–2.0 kg rainbow trout (*Salmo gairdneri*) after intravenous injection of Fraction 1 or saline. All figures in the table are in terms of white cells per cubic millimetre of blood times 10^{-3}. Fish no. 1–8 received 1.13 mg of Fraction 1 (measured as hexose) in 0.2 ml of physiological saline; fish no. 9–13 were saline controls; these fish received 0.2 ml of physiological saline. NC = no count made.

Fish no.	Hours postinjection				
	5	24	48	72	120
1	8.3	8.5	27.7	51.4	25.1
2	7.1	8.9	31.5	48.0	26.8
3	6.7	8.7	33.0	57.6	33.4
4	8.9	9.0	42.0	66.3	32.2
5	7.9	9.6	32.4	54.8	32.0
6	9.0	9.2	38.7	47.6	23.4
7	9.9	8.8	29.1	48.1	26.6
8	8.8	9.1	31.2	53.2	26.4
9	25.0	30.6	21.4	22.1	NC
10	39.3	31.8	29.5	39.7	NC
11	32.1	31.9	32.5	30.8	NC
12	26.3	28.2	29.3	31.0	NC
13	27.2	39.0	40.1	33.3	NC

TABLE 3. Increase in the susceptibility of small coho salmon (*Oncorhynchus kisutch*) (8–13 cm long) to *Aeromonas salmonicida* by the LCL factor. Bacterial dose injected was about 63 cells. LCL injected was about 0.04 mg as hexose. All injections were made in a volume of 0.2 ml.

Day no.	No. fish that died after injection of[a]			
	Saline plus *A. salmonicida*		*A. salmonicida* plus LCL factor	
	Subgroup		Subgroup	
	A	B	A	B
1	0	0	0	0
2	0	0	0	0
3	4	1	13	11
4	3	4	3	3
5	1	1	1	2
6	0	0	1	1
7	0.	0	0	0
8	0	0	0	1
9	0	0	0	0
10	0	0	0	0
Fraction dead on day 10	8/20	6/20	18/20	18/20
No of positive cultures at autopsy	8	6	18	18

[a]No deaths from injection of saline alone or saline plus LCL factor.

was recovered from all of them, but not from the few survivors.

Thus, the experiment established the fact that the injection of LCL or Fraction 1 together with a minimum dose of *A. salmonicida* enhanced the pathogenic effect of the bacterium and resulted in a significant increase in the percent mortality of small coho salmon compared to that produced by the organisms alone. Presumably, it exerted this effect by increasing the susceptibility of the host and may well be regarded as one of the virulence factors of *A. salmonicida*.

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Aspects of Predation of Seals by Polar Bears

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STIRLING, I., AND W. R. ARCHIBALD. 1977. Aspects of predation of seals by polar bears. J. Fish. Res. Board Can. 34: 1126–1129.

Data were collected from 227 ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) killed by polar bears (*Ursus maritimus*) in the western arctic and the eastern high arctic. During periods of high ringed seal productivity, pups constituted at least half of the seals killed in both areas during the spring. Bearded seals were taken less often than ringed seals in both areas but were more important as prey to polar bears in the western arctic. Carcass utilization was significantly higher in the eastern high arctic than in the western arctic although the reason was not apparent. Scavenging of unutilized seal remains is probably of great importance to the survival of large numbers of arctic foxes (*Alopex lagopus*) through the winter.

Key words: *Ursus maritimus*, *Phoca hispida*, *Erignathus barbatus*, predation, interspecific relationships, Arctic Ocean mammals

STIRLING, I., AND W. R. ARCHIBALD. 1977. Aspects of predation of seals by polar bears. J. Fish. Res. Board Can. 34: 1126–1129.

Nous avons cueilli des données sur 227 phoques annelés (*Phoca hispida*) et phoques barbus (*Erignathus barbatus*) tués par des ours polaires (*Ursus maritimus*) dans l'Arctique occidental et le Haut-Arctique oriental. En périodes de forte productivité des phoques annelés, les chiots constituent au moins la moitié des phoques tués dans les deux régions au printemps. Les phoques barbus sont capturés moins souvent que les phoques annelés dans les deux régions, mais ceux-là sont plus importants que ceux-ci comme proies des ours polaires dans l'Arctique occidental. Les carcasses sont utilisées à un degré significativement plus élevé dans le Haut-Arctique oriental que dans l'Arctique occidental, quoique la raison n'en soit pas apparente. Les phoques non utilisés ont probablement une grande importance pour la survie d'un grand nombre de renards arctiques (*Alopex lagopus*) durant l'hiver.

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ALTHOUGH it is common knowledge that polar bears (*Ursus maritimus*) eat seals, there is little quantitative information available on the age structure of the seals caught relative to that of the available prey population, the importance of geographic or seasonal variations in their numbers, and the relative importance of other potential prey species. This paper summarizes field data collected by the Canadian Wildlife Service from seals killed by polar bears in the Canadian arctic from 1971 through 1975.

Materials and Methods

From 1971 through 1975 the Canadian Wildlife Service conducted mark and recapture programs on polar bears in the western arctic and the eastern high arctic (Stirling et al. 1975, 1977b). These involved extensive aerial searching of coastal areas of the northern mainland and the arctic islands and over the associated offshore sea-ice areas. Most of the field work was conducted during April and May when most of the offshore ice was frozen solid except for lead systems in some areas. Subjectively, we estimate that at least 80% of the areas searched for bears were completely frozen. There was often snow on the ice, which facilitated tracking of bears with a helicopter.

When the sea ice is frozen, ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) use the heavy claws of their foreflippers to scratch the ice and maintain breathing holes in the last cracks when they freeze. Drifting snow accumulates along these cracks and pressure ridges and covers the breathing holes. In late March to early April female ringed seals dig subnivean lairs above their breathing holes, in which they give birth to and suckle their pups (Smith and Stirling 1975). Consequently, through the winter and into late spring, bears must break through the often thick snow drifts to gain access to the seals. Thus, when following the tracks of a single bear or family of bears, the number of

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TABLE 1. Age structure of ringed seals killed by polar bears in spring.

	Killed on completely frozen ice					Killed on pack or floe edge				
	Pup	(Subadult) 1–5 yr	Adult	Unknown	Total	Pup	(Subadult) 1–5 yr	Adult	Unknown	Total
W arctic										
1971–73	17	10	4	3	34	0	5	1	0	6
1974–75	0	5	30	22	57	0	1	0	1	2
E high arctic										
1972–75	67	11	11	10	99	2	4	1	0	7

successful and unsuccessful attempts to dig out seals were recorded. From the air it was usually easy to spot where a kill had been made because of blood or other remains on the snow. Seals killed along the floe edge or in the pack ice were usually located by finding the carcass or blood spots in the snow.

Whenever a seal kill was located, the site was examined and notes were made on the species killed, the habitat, the time and weather if the kill was fresh, how the seal was killed if it could be deduced from the tracks, and evidence of scavenging. The degree of utilization of the whole weight of the carcass was estimated visually. Whenever possible, teeth or claws from the foreflippers were collected to facilitate age determination (McLaren 1958; Stirling et al. 1977a).

From 1971 through 1975, data were collected from 227 ringed and bearded seals killed by polar bears in the western arctic and eastern high arctic during the spring and from 17 killed during the summer and fall. The data were segregated into three groups: eastern high arctic 1972–75; western arctic 1971–73; and western arctic 1974–75. The eastern and western arctic areas were segregated to look for possible geographic variation. The western arctic sample was divided because of a major decline in the numbers of seals and bears that took place in 1974 and 1975 (Stirling et al. 1977a). We wished to determine whether or not there were differences during the period of decline in the species of seals captured, the degree of utilization, and in hunting efficiency.

Results and Discussion

Table 1 presents the age structure of 205 ringed seals killed by polar bears in the spring, 190 of which were killed at either breathing holes or birth lairs. During 1971–73 in the western arctic, when ringed seals appeared to be more abundant and productivity was higher than in 1974–75 (Smith and Stirling 1975; Stirling et al. 1977*a*), 54.8% of the seals (that could be aged) found killed by polar bears in the fast ice areas were pups. The proportion of pups in this habitat was significantly greater (75.3%) in the eastern high arctic spring sample ($\chi^2 = 4.57$; $P < 0.05$). During 1974–75 in the western arctic, when ringed seal productivity was low, no pups were identified in the sample of seals killed by polar bears. Clearly, during periods of high ringed seal productivity, pups constitute a high proportion of the seals killed in both areas during the spring. Two thirds (10/15) of the total number of ringed seals found killed in the pack ice or along the floe edge were subadults but the sample sizes were too small to permit further analyses.

There was a significant increase (85.7% of the seals found killed that could be aged vs. 14.8%) in the proportion of adult seals in the kill in the western arctic in 1974–75 compared to 1971–73 ($\chi^2 = 34.89$; $P < 0.01$) and similarly in the proportion of unaged seals in the total sample (38.6% vs. 8.8%) ($\chi^2 = 9.47$; $P < 0.01$). Presumably, under normal circumstances, the pups and subadults form the largest proportion of the kill because they are less experienced and consequently more easily caught. Newly weaned pups and subadults may also be spatially segregated into areas where they are more vulnerable to predation but we have no direct evidence of this. In the samples of bearded seals killed by polar bears, the proportion of adults was higher in 1974–75 than in 1971–73 (50%:20%) but the sample sizes were too small to permit further analyses (Table 2). Clearly, bearded seals are taken less often than ringed seals (Tables 1 and 2). However, the bearded seals taken are of greater importance than the numbers alone indicate because, on average, they are at least double the size of the ringed seals. The proportion of bearded seals in the eastern high arctic sample

TABLE 2. Age structure of bearded seals killed by polar bears in all habitat types.

	Pup	1–4 yr	Adult	Unknown	Total
W arctic					
1971–73	0	4	1	0	5
1974–75	1	4	5	4	14
E high arctic					
1972–75	0	1	0	2	3

was significantly lower than from either western arctic sample (1971–73, $\chi^2 = 4.52$; $P < 0.05$; 1974–75, $\chi^2 = 13.93$, $P < 0.01$). Therefore, bearded seals are apparently more important in the diet of polar bears in the western arctic than in the eastern high arctic. Although the proportion of bearded seals in the western arctic sample was larger in 1974–75 than in 1971–73 (19.2% vs. 11.1%) the difference was not significantly different ($\chi^2 = 1.34$; $P > 0.20$). This might have been expected, since Stirling et al. (1977a) suggested that the numbers of bearded seals decreased by about the same proportion as did the ringed seals in 1974–75 (56.6 and 48.2%, respectively).

The polar bear that kills a particular seal often abandons a substantial portion of the carcass (Stirling 1974; Stirling and McEwan 1975). Often it was difficult to evaluate the degree of utilization of many of the carcasses because of scavenging after the original bear(s) had departed and because snow sometimes obscured the tracks around the kill. Observations on the undisturbed behavior of wild polar bears indicated that scavenging by other bears often took place within a short period of time after the seal was killed, not infrequently to the point where a seal was taken away from the bear that killed it by a more dominant bear (Stirling 1974, unpublished data).

Scavenging by arctic foxes (*Alopex lagopus*) was common throughout the year and by ravens (*Corvus corax*) and gulls (*Larus* sp.) during the summer. In the eastern high arctic, five instances of scavenging by wolves (*Canis lupus*) were recorded and in a letter to the Canadian Wildlife Service dated February 6, 1967, M. Curtis of MacDonald College, Montreal, documented what he believed to be two instances of wolves preying on seals, based on his interpretation of tracks in the snow. Smith (1976) has documented extensive predation by arctic foxes on ringed seal pups in their subnivean lairs. These observations show that in some cases it may not be clear whether the bear was the predator or the scavenger. The percent of the whole carcass that was utilized could still be estimated, however.

Thus, while recognizing the errors incurred, estimates were made of the percent of utilization of carcasses (excluding fresh ones that bears were still feeding upon) at the time they were found (Table 3). Carcass utilization in the eastern high arctic during 1972–75 was significantly greater than in the western arctic during both 1971–73 ($t = 6.24$, df = 133, $P < 0.01$) and 1974–75 ($t = 2.42$, df = 127, $P < 0.05$). Presumably because seals were less abundant in the western arctic in 1974–75 than in 1971–73, a significantly higher proportion was consumed of those that were caught ($t = 2.31$, df = 64, $P < 0.05$). The increase in the proportion of unaged seals in the western arctic in 1974–75 (Table 1) probably resulted from the greater degree of utilization of and scavenging upon the carcasses, which consequently made it more difficult to find specimens for age determination. Even so, on the average, 20% of the carcasses by weight (but not necessarily of the caloric value) were not consumed before we found them in 1974–75. In 1973 four of the pups we found killed in the western arctic were not eaten at all. (Stirling and McEwan 1975), something not recorded in the eastern high arctic. Why the degree of utilization of the seals killed by polar bears should be lower in the western arctic than in the eastern high arctic is unclear. However, the fact that it does occur is further attested to by the large numbers of foxes that survive the winter apparently by scavenging in the western arctic and consequently form the basis of a substantial arctic fox trapping industry (Smith 1976; Stirling et al. 1977a). This does not apparently occur to nearly the same degree in the eastern high arctic.

Table 4 compares success rates of polar bears hunting seals at subnivean breathing holes and birth lairs in the western arctic and eastern high arctic. The range in the proportion of successful attempts (6.4–8.6%) did not vary significantly between the samples ($\chi^2 = 0.88$, $P > 0.8$). It was particularly interesting that the proportion

TABLE 3. Percent utilization of carcasses of seals killed by polar bears.

	Ringed seal			Bearded seal		
	N	$\bar{x}$	SD	*N*	$\bar{x}$	SD
W arctic						
1971–73	36	60.83	38.22	5	32.00	16.31
1974–75	30	80.50	29.11	8	89.38	19.73
E high arctic						
1972–75	99	91.06	17.85	3	63.33	28.97

TABLE 4. Success rates of polar bears hunting seals at subnivean breathing holes and birth lairs.

	Attempts	Successes	% Successes
W arctic			
1971–73	556	48	8.6
1974–75	120	8	6.7
E high arctic			
1972–75	172	11	6.4

of successful attempts remained the same in the western arctic 1974–75 when far fewer attempts were found despite the fact that similar or greater areas were searched (Stirling et al. 1975). Smith et al. (1976) reported a slightly higher success ratio (21/205 – 10.2%) from the eastern high arctic in 1975, although it was still not significantly greater than in 1972–74 (6.4%) ($\chi^2 = 1.78$, $P > 0.2$). These success rates for spring hunting at subnivean breathing holes are much higher than those observed by Stirling (1974) during the summer on the bare sea ice (<2% success on 288 hunts observed). In comparison, Smith (1976) noted that of 370 ringed seal lairs examined in Amundsen Gulf and Prince Albert Sound, 113 (30.5%) had been entered by arctic foxes. In the springs 1973 and 1974, his estimates of fox predation on newborn ringed seal pups ranged between 21.1 and 57.7%. Considering how high the rates of predation on pup and older seals at subnivean breathing holes and birth lairs in the spring can apparently be, predation is clearly a more significant mortality factor for the ringed seals than was previously thought.

The summer sample of only 17 seals killed by bears, 9 of which could not be aged, was too small to draw any conclusion. More summer kill data are required before any analysis of seasonal variation can be done.

Various authors have commented on polar bears attacking and possibly killing white whales (*Delphinapterus leucas*) and walrus (*Odobenus rosmarus*) (Degerbøl and Freuchen 1935; Freeman 1973; Heyland and Hay 1976). An adult hooded seal (*Cystophora cristata*) was killed by a polar bear in Radstock Bay, southwestern Devon Island in 1973. However, the results of our field work to date suggest that these other marine mammal species are probably of limited importance to polar bears compared to ringed and bearded seals.

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A Simple Mechanism that Causes Collapsing Stability Regions in Exploited Salmonid Populations

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PETERMAN, R. M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Board Can. 34: 1130–1142.

Depensatory predation mortality on salmon when added to a Ricker production model can create a system with at least two stable equilibria and two domains of attraction. The behavior of such a fish system is different from a single equilibrium situation and a simple mechanism is described through which commercial exploitation changes the ability of such multiple-equilibrium fish populations to respond to perturbations in survival rates. Furthermore, it is shown that this change in size of stability regions is proportional to the exploitation rate and that classically defined maximum sustainable yield (MSY) exploitation rates are inevitably close to the rates that would cause a drastic decrease in the population. The uncertainties inherent in environmental effects on survival and in achievement of desired exploitation rates precipitate the need to back away from the usual MSY exploitation rates and set up (through enhancement) a system of stocks whereby feedback information is provided to the manager. This approach of adaptive management seeks reasonable yields while gaining information about the state (or changes in state) of the system. Some applications of catastrophe theory are discussed, especially with reference to harvesting multiple-stock salmon systems.

Key words: stability, resilience, exploitation, salmon, depensation, multiple equilibria, adaptive management, enhancement, catastrophe theory

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La mortalité par prédation dépensatoire sur le saumon, ajoutée à un modèle de production de Ricker, peut créer un système possédant au moins deux équilibres stables et deux domaines d'attraction. Le comportement d'un tel système pour les poissons diffère d'une situation à un équilibre, et nous décrivons un mécanisme simple en vertu duquel l'exploitation commerciale change l'aptitude de telles populations de poissons à équilibre multiple à répondre aux perturbations des taux de survie. De plus, nous démontrons que ce changement dans l'étendue des régions de stabilité est proportionnel au taux d'exploitation, et que les taux d'exploitation classiquement définis comme rendement maximal soutenable (RMS) se rapprochent invariablement des taux qui causeraient une diminution dramatique dans la population. A cause des incertitudes inhérentes aux effets de l'environnement sur la survie et à la poursuite des taux d'exploitation désirés, il devient de plus en plus urgent de s'éloigner des taux d'exploitation correspondant au RMS usuel et d'établir (par revalorisation) un système de stocks selon lequel le gestionnaire recevra un retour d'information. Cette approche de gestion adaptive cherche à obtenir des rendements raisonnables tout en apprenant davantage de l'état (ou changement de l'état) du système. L'auteur examine certaines applications de la théorie de la catastrophe, surtout en rapport avec la récolte de systèmes de saumons à stocks multiples.

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HOLLING (1973) argues from theoretical and empirical grounds that it may prove useful if ecologists modify their viewpoint of stability of ecological systems. Historically, the main focus of attention has been on equilibria, but we know that in the real world, equilibria are rarely, if ever, achieved. Natural systems are constantly subjected to fluctuating conditions that cause changes within the system. Often these fluctuations exceed the limits of a system's ability to respond and the system becomes distinctly different in character through extinction or drastic long-term changes in abundance. Holling concludes that we should concentrate on these limits to system response, rather than on equilibria.

Those natural systems that can cope successfully with wide ranges of fluctuations in state

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variables, driving variables, or parameters are more "resilient" than systems with narrower tolerance ranges (Holling 1973). There are numerous mechanisms affecting a system's resilience: for example, shapes of reproduction and survival functions, types of dispersal characteristics, and existence of areas of inaccessibility to predation (refugia). Holling (1973) suggests that one effect of man's activities may be to reduce the resilience of ecological systems by shifting the boundaries or limits of stability and Ricker (1963) investigates an example of changing stability bounds caused by shifts in fish population age structure.

This paper describes another simple man-induced mechanism that reduces the size of stability domains in commercially exploited salmon populations, and the management implications of this mechanism are explored in depth.

Background

Ricker (1954) noted when he introduced the stock–recruitment concept that the existence of depensatory mortality processes (defined by Neave (1953) as processes causing higher percentage mortality at low prey population densities) might result in the replacement line crossing the recruitment curve in three places; instead of one equilibrium, there would be three (Fig. 1). Two of these equilibria (points A and C) are stable, that is, the spawning population tends to move toward one or the other value. Point B, on the other hand, is a transient or unstable equilibrium; the population moves away from this level. Thus, the spawning population size corresponding with point B forms the boundary (X_0) between two different domains of attraction. Spawning populations in any one domain tend to remain there unless pushed across this boundary. The evidence for existence of more than one equilibrium or domain of attraction in real fish populations comes from two sources: data showing temporal changes in fish populations and knowledge of the form of the processes that cause these changes.

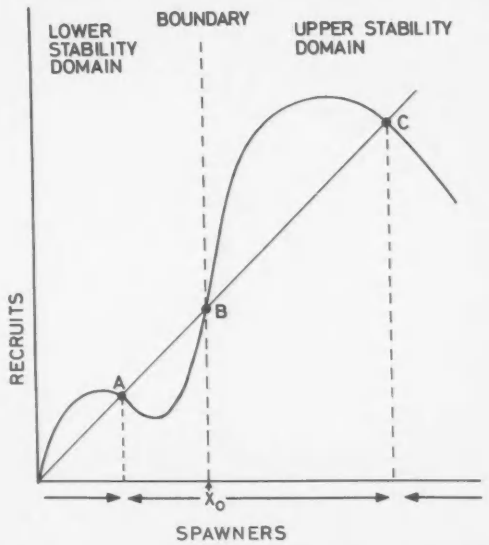

FIG. 1. A recruitment curve showing the effect of depensatory mortality (after Ricker 1954, fig. 30). See text for explanation.

First, there are numerous examples of populations that dropped to very low levels and that failed to recover to former high levels, even after the causes of the stock collapses were removed (see Beeton 1969; LeCren et al. 1972; Holling 1973). Such examples suggest the existence of upper and lower domains of attraction for these populations.

Perhaps one of the best illustrations of the existence of multiple equilibria or domains of attraction comes from the history of the pink salmon (*Oncorhynchus gorbuscha*) on the Atnarko River in British Columbia. The odd-year population (total catch plus escapement) on this river dropped from a high of about 2.5 million in 1961 to about 80,000 in 1967 due to a combination of overexploitation and poor weather conditions (F. E. A. Wood and R. Hilland, Fisheries and Environment Canada, unpublished data). The population has remained at this very low level for five consecutive cycles (Fig. 2), despite the fact that the exploitation rate has dropped considerably and that environmetnal conditions have been relatively good. It is notable that the even-year Atnarko pinks, which spawn in the same area, have remained high during the past five cycles, showing that the low odd-year population is not being held down by major alterations in spawning habitat conditions. The mechanism that keeps the odd-year cycle population small is not known; it could be the interaction between odd- and even-year cycles through adult predation on outgoing young or through deterioration of spawning grounds by masses of dead even-year eggs. However, the exact mechanism is not important for the purpose of this paper. What is significant is the apparent existence of two distinct domains of behavior, one for small population sizes and one for large populations.

Next, Paulik (1973) and Holling (1973) illustrate how multilife stage, density-dependent processes such as predation can result in recruitment curves that cross the replacement line at several points. There is extensive evidence in the salmonid

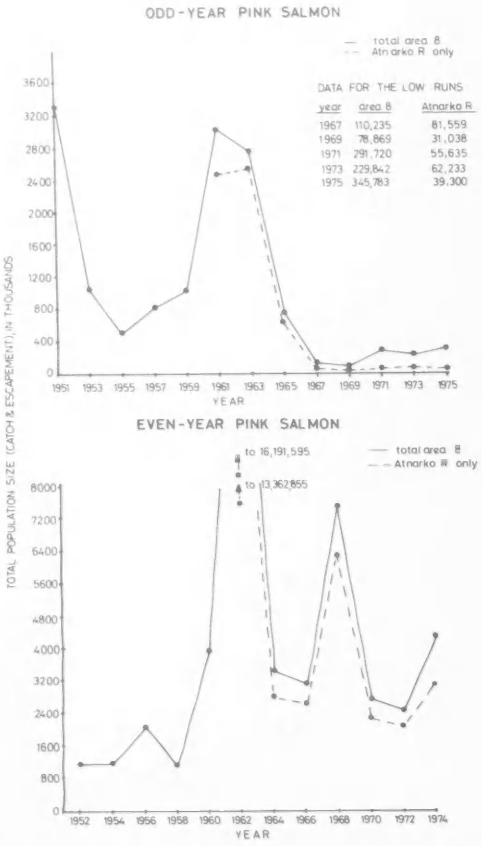

FIG. 2. Total population data (catch plus escapement) for the pink salmon (*Oncorhynchus gorbuscha*) of the Atnarko River, B.C. and total Area 8 pinks (which includes Atnarko River). Note that while Atnarko River data have been separated only since 1961, this stock has constituted most of the total Area 8 population, which has been counted back to 1951.

literature showing that predation mortality on young salmon can be as high as 65–85%, with the highest percentage mortalities occurring at low prey population densities (Hunter 1959; Neave 1953; Ricker 1962). As will be illustrated later, this magnitude of depensatory mortality, when combined with the other sources of mortality, can be sufficient to create the multiple-crossover phenomenon discussed by Paulik and Holling, at least for some exploited systems if not for unfished situations.

Thus, the theoretical and empirical evidence implies that some, but not all, fish populations may have recruitment curves with two or more potential equilibria, and therefore more than one domain of attraction. Clearly, fisheries managers dealing with such multiple-equilibrium situations would like to keep populations in the upper domain by avoiding the boundary shared with the lower domain. If the boundary were static, this task might be relatively simple, but this boundary shifts in response to man's interventions as well as environmental changes. Ricker (1954) noted that as the exploitation rate on a population increases, the slope of the new replacement line increases accordingly (Fig. 3), and that even if there is not more than one equilibrium when the stock is unexploited there could be two or more when there is harvesting. Note that recruits here mean recruits before harvest. The critical implication for management is that the spawning or boundary population size below which the stock drops into the lower region of stability increases from X_0 to X_0' when the exploitation rate is increased to 30%, for example.

This paper investigates the management consequences of changes in exploitation rate and subsequent shifts in this boundary and in sizes of stability domains. In addition, some effects of altering reproduction parameters (through enhancement, for example) will be discussed.

The Model

The theoretical species used for this study resembles pink salmon, which has a simple age

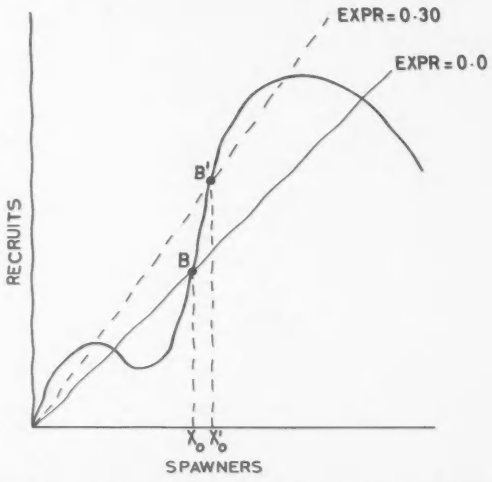

FIG. 3. Same recruitment curve as in Fig. 1. When the exploitation rate on the recruits (EXPR) is raised from 0 to 30%, the slope of the replacement line changes accordingly. The location of the transient equilibrium changes from B to B', and the boundary population size changes from X_0 to X_0'.

structure and discrete generations. Offspring (fry or smolt) production is assumed to be described by a Ricker stock–recruitment curve, an assumption supported by some salmon data (e.g. Skud 1973). Losses to predation on the downstream migration, in the rearing lake, in the estuary, or in the ocean are removed from the resulting offspring population to give net recruits, or returning adults. It is assumed that a constant proportion of the offspring surviving predation will return as adults. It can be shown that the general conclusions of this study would be the same if a Beverton and Holt model (1957) had been used instead of the Ricker model, as long as depensatory mortality due to predation had been added in the same way.

The basic model used was:

$$(1) \quad R = S \exp [A(1 - S/E)]$$

$$(2) \quad N = R - [(B \cdot R^2)/(P^2 + R^2)]$$

where R = number of offspring before predation losses, S = number of spawners, A = the reproduction parameter of the Ricker model, E = the unfished equilibrium population size, before effects of predation are added, N = net number of recruits after predation losses but before harvest, B = the maximum number of fish that could be removed by the total predator population (maximum ration per predator times number of predators), P = the number of prey that results in $B/2$ prey lost to predation.

Predation can be measured in terms of the functional response, defined by the number of prey eaten per predator per unit time as a function of the number of prey available. Holling (1965) describes several basic forms for this relationship and two are relevant to the present situation. The so-called Type II functional response (Curve a in Fig. 4) describes the situation for predators that do not have learning characteristics. The number eaten increases with increasing prey numbers, but begins to asymptote as the predator begins to reach its capacity for processing prey (due to limited handling time). Thus, above a certain number of prey, each predator can only take a maximum number of prey. The Type III or S-shaped functional response (Curve b in Fig. 4) is characteristic of predators that learn. At low prey numbers, the predators may need some experience before "switching on" to the prey, but once this has occurred the number eaten increases more rapidly with increasing prey than in the Type II response. However, these predators are subject to the same handling time limitations and an asymptote is soon reached.

The predation term of equation (2) above produces the Type III functional response and has the two biologically relevant parameters indicated, B and P (C. S. Holling, personal communication). There are several ways to justify using the Type III instead of the Type II functional response. First, the predators of salmon fry are largely vertebrates (fish) which, according to Holling (1965), should show S-shaped functional responses because of their learning, forgetting, and switching characteristics. Second, an individual predator with a Type II (concave) functional response may actually have a zero attack rate at a nonzero prey density, thereby effectively creating a refugium for the prey (Curve c in Fig. 4). This turning-off point (the prey density below which there are no attacks) is probably not constant among all predators in a population; if it is assumed to be normally distributed among the predators, then the aggregate functional response of the total predator population will be an S-shaped (Type III) curve (C. J. Walters, University of British Columbia, personal communication). Finally, any tendency for predators to aggregate (a quick numerical response) will also result in a Type III functional response (Hassell and May 1974). Murdoch and Oaten (1975) show how an S-shaped predation function gives rise to the type of "depensatory recruitment curve" illustrated graphically by Ricker (1954, 1962).

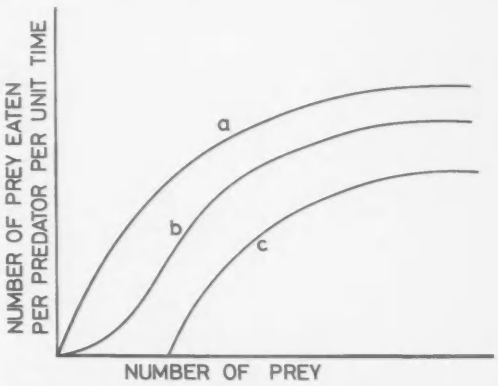

FIG. 4. Example predator functional responses. Curve a is a Type II response, Curve b is a Type III response, and Curve c is a Type II response but with a nonzero intercept. All three types could in reality asymptote at the same level; they are drawn here with different asymptotes merely to illustrate the differences in forms.

However, an S-shaped functional response of individual or a population of predators is not necessary to create a recruitment curve with more than one stable equilibrium; predators

having a Type II functional response with a non-zero intercept on the prey axis would suffice (Curve c in Fig. 4). Below that intercept, net gains in the prey population would become possible, compared with net losses at some higher prey densities.

The present model implicity assumes the predator population size is relatively constant through time and independent of the prey population, a reasonable assumption for pink and chum salmon (*O. keta*) prey, since the salmon fry are a food source for only a short period of time during downstream migration in any year.

The few studies that exist show that the percent predation mortality on young salmon is highest at relatively low prey densities (Foerster 1968; Hunter 1959; Neave 1953; Ricker 1962) and therefore the "dip" in the net recruitment curve occurs at these low levels. To illustrate more clearly the graphical effects of depensatory mortality, the recruitment curves in Fig. 1, 3, and 6 have been drawn with the "dip" slightly exaggerated.

Methods of Analysis

The model used here cannot be solved analytically for S (nor can the Ricker model), so to determine the location of the boundary between the two domains of stability for any sustained exploitation rate, it is necessary to solve for the sustainable harvest rate corresponding to any given boundary population size. For a given S, the net number of recruits (N) is calculated, giving a slope of N/S for the line connecting that point on the recruitment curve with the origin. Ricker (1958a) notes that the relation between this slope (M) and its corresponding sustainable exploitation rate (H) is:

$$(3) \quad H = 1 - (1/M)$$

Therefore, each boundary population size X_0' can be associated with a particular sustainable exploitation rate. Finally, the maximum sustainable yield (MSY) harvest rate is determined by iteratively searching along the net recruitment curve for the point where it is the greatest vertical distance from the replacement line (Ricker 1973b).

Unless otherwise noted, the parameter values for all examples in this paper are as follows: $A = 1.6$; $E = 500{,}000$; $B = 150{,}000$; $P = 90{,}000$. These parameter values create a lower, stable equilibrium at about 20,000 spawners, or 4% of the upper equilibrium, perhaps a conservative estimate compared to the Atnarko River pink salmon or other situations. The resulting model was analyzed for deterministic and stochastic cases.

Results and Discussion

Single Stock, Deterministic Case

Figure 5 shows that the population size corresponding to the boundary between the two

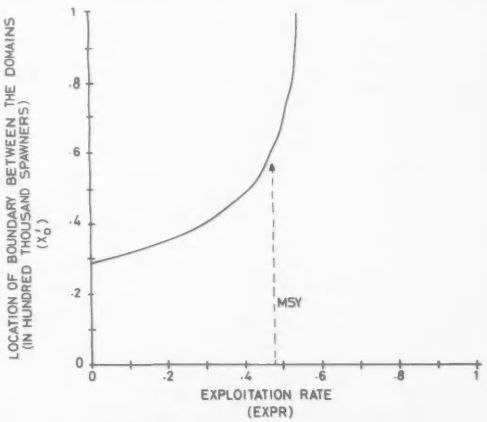

FIG. 5. Relation between X_0', the boundary between the two domains of stability, and exploitation rate. The dotted line designates the MSY exploitation rate for that stock (biological parameters given in text).

domains of stability increases sharply as high harvest rates are approached. Because the size of the lower domain increases as the exploitation rate increases, the proportion of spawning population sizes that will be in the lower domain increases dramatically. However, the most significant point for management is that the MSY exploitation rate comes dangerously close to the steeply rising portion of the curve (Fig. 5). Ricker (1973a) states that during the course of the development of fisheries, populations often are temporarily overexploited as the managers "zero in" on MSY (putting the system temporarily farther out on the ascending limb of the curve in Fig. 5). In such cases, an incremental change in natural mortality or in exploitation rate (possibly caused by increased gear efficiency) can cause greater alteration in the proportion of fish population sizes that are in the lower domain than the same unit change at lower exploitation rates. Ricker (1963) noted a similar nonlinear effect dealing with changes in population age structure.

These discussions assume a fixed exploitation rate that results in a population remaining forever in the lower stability region once it gets below the boundary associated with that harvest rate. However, in order to get the population back in the upper domain, the location of the boundary can be changed by altering the exploitation rate. But the exploitation rate must be dropped quickly enough to "catch" the population before it goes below the depensation level for the no-harvest case (X_0). The shape of the curve in Fig. 5 implies that at high harvest rates only a small reduction in harvest rate may be necessary to

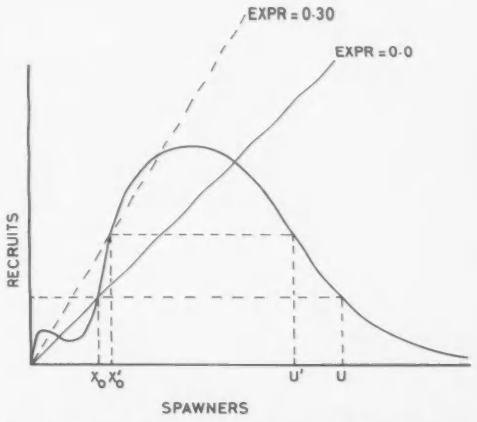

FIG. 6. Where there is strong density dependence in a stock, spawning populations greater than U will, on average, produce X_0 or fewer recruits, putting the population into the lower domain of stability in the next generation. When exploitation of recruits is increased above 0.0, the lower and upper bounds of the "desired" region change to X_0' and U', respectively, shrinking the size of that region.

achieve a given reduction in the boundary limit. Just how quickly harvest rates can be reduced in actual practice depends upon social and economic pressures as well as changes in gear efficiency. However, the significant management conclusion is that the process of changing sizes of stability domains is a highly nonlinear one. A discussion of how the foregoing applies to stocks having fluctuating survival rates will be held until a later section of this paper.

This simple case only considers the dynamics of low populations in the region where depensatory processes are important. However, we also need to examine the results of having large spawning populations if there are strong density-dependent (compensatory) processes operating at any life stage of the fish. In these cases, there may be very few recruits resulting from large spawning populations, causing the population to drop into the lower domain of stability, even in the absence of any exploitation (Fig. 6). This "reflection" of the lower region of stability on the right end of the recruitment curve has similar properties to the lower region; as the exploitation rate is increased, the boundary of this upper "reflected" region, U, is reduced to U' (see Fig. 6). The existence of the effect of this "reflection" of the lower domain of stability is consistent with, though it does not necessarily always explain, the commonly observed large recruitment just prior to collapse of fish populations such as in Peruvian anchovetas (Parrish 1973; Anon. 1974).

The region that management desires the population to occupy thus becomes bounded on both ends by spawner levels that lead the population to the lower domain of stability within the next generation. Increasing exploitation rates increase the lower bound and decrease the upper bound, thereby shrinking the size of this range of desired population sizes. Figure 7 shows, for a reproduction curve with the parameter values given earlier, how the size of this region changes as a function of the exploitation rate. When the system is at MSY exploitation rate, the size of the domain is <65% of the size of the domain at an exploitation rate of zero. Furthermore, at the maximum possible sustainable exploitation rate (which is greater than MSY harvest rate but with low yield), the region's size is <45% of the size in the unexploited case. The spawning populations at which this phenomenon becomes important are, for the case illustrated in Fig. 7, much higher than the unfished equilibrium, but this is not true for all parameter combinations. Thus, the general characteristic of shrinking domains is probably of significance to managers. Again note that the MSY harvest rate falls very near the point at which the region's size collapses rapidly. Conclusions from this analysis are the same as before; fisheries operating near MSY harvest rates have much higher probabilities of dropping into lower domains of stability than might be intuitively expected, especially when uncertainties in exploitation and reproductive rates are taken into account (next section).

The conclusion resulting from the reflection of the depensatory effect onto the right limb of the recruitment curve does not, of course, apply to

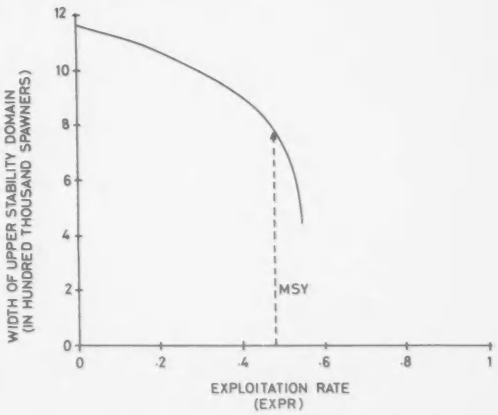

FIG. 7. The size of the domain of stability (delineated by X_0' and U' in Fig. 6) as a function of exploitation rate. Domain width is in number of fish, $U' - X_0'$. Arrow indicates MSY exploitation rate for this stock.

the case where a saturating model such as the Beverton–Holt describes the production of offspring, because in such a model there is no decrease in production at high numbers of spawners.

The catch curves for several single-stock, deterministic cases represent the above information in a different form. Figure 8 shows the relation between sustainable catch and exploitation rate for a family of depensatory recruitment curves with different A values. Because the effect of depensation has been included in the model, these catch curves break off at a certain exploitation rate. Above this exploitation rate, the stock becomes overexploited and there is either zero sustainable catch or a very small catch (if the population persists in the lower domain).

Single Stock, Stochastic Case

The deterministic recruitment curve above only calculates recruits resulting from a given number of spawners under average environmental conditions. Variation in environmental factors affecting reproductive output or survival is introduced into the model using the log-normal, multiplicative form argued for by Allen (1973) and Walters (1975),

$$V = \exp(G)$$

where G is a number drawn randomly from a normal distribution having a mean of 0.0 and a SD of 0.6. The distribution of the resulting environmental factor is similar to that of "Level A variability" of Ricker (1958b) and Larkin and Ricker (1964).

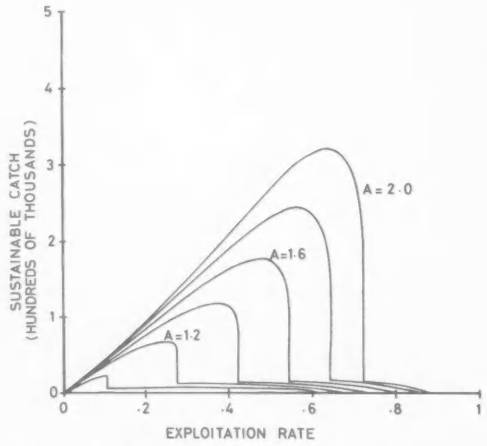

FIG. 8. The sustainable catch of stocks with A values ranging from 1.0 to 2.0 at intervals of 0.2 as a function of exploitation rate.

Equation (2) thus becomes

$$(4) \quad N = V \cdot \{R - [(B \cdot R^2)/(P^2 + R^2)]\}$$

This survival factor shifts the net recruitment curve up or down, which causes a change in the location of the boundary between the upper and lower domains of attraction (Fig. 9). As V increases (environment becomes more suitable), the boundary population size decreases and the lower domain shrinks (Inset, Fig. 9). If the distribution of environmental factors is known, the statistical distribution of boundaries can be determined for any given exploitation rate and confidence bands can be calculated for the curves which describe where we expect to find the boundary (Fig. 10). Note that the boundary between the two domains never gets below 20,000 because the upper and lower domains merge into one domain when the environmental factor and exploitation rate get above certain levels, i.e. only the lower equilibrium exists.

This information on shifts in boundaries due

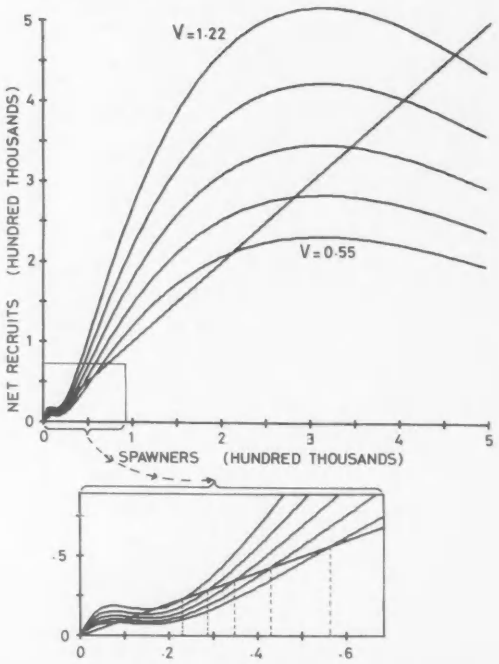

FIG. 9. Changes in the multiplicative environmental factor that affects recruits, as applied in this model, shift the whole recruitment curve and also its replacement line crossover points (dotted lines in the inset). Different values of V ranging from 0.55 to 1.22 were chosen to demonstrate some of the range of changes in the curve.

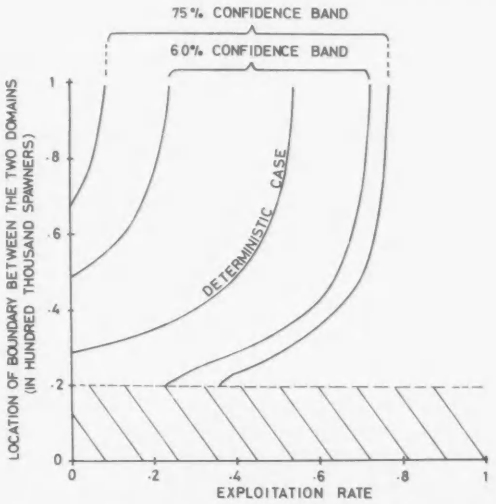

FIG. 10. The 60 and 75% confidence bands around the deterministic location of the lower bound using the distribution of survival factors described in text. In the hatched region, there exists only a single domain of attraction, in this case the lower domain.

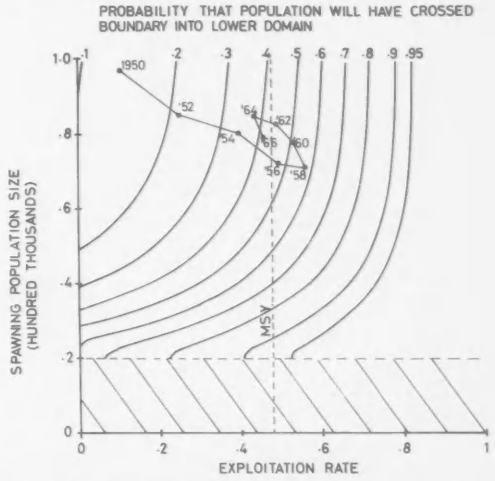

FIG. 11. The contours give the probability that a spawning population will cross into the lower domain if a given exploitation rate is applied to its offspring. Superimposed on these contours is the time course of a hypothetical developing fishery, similar to the events observed by Ricker (1973a) and Schaaf (1975). Note that as the MSY exploitation rate (vertical dotted line) is temporarily exceeded, the probabilities of the population being below its lower bound are relatively high. In hatched area, there exists only a single domain of attraction, in this case, the lower domain.

to changing environmental conditions can be presented in another form (Fig. 11), an isopleth diagram which shows the probability of any given spawning population causing the next generation to be in the lower domain, given the exploitation rate to be imposed on the offspring (this rate permits calculation of the replacement line's slope). This isopleth diagram can be useful to managers if the temporal sequence of environmental factors affecting offspring survival is unknown but their historical distributions are known, because it clearly illustrates the maximum exploitation rate that should be allowed to keep the fish population above the boundary with a given risk (a risk which can vary between different managers or situations).

The historical development of a hypothetical fishery can be traced on this isopleth diagram and population collapses can be interpreted in terms of domains of stability (Fig. 11). The classical course of events which has been observed in developing commercial fisheries (Ricker 1973a; Schaaf 1975) traces a spiral on this graph, where initial overshooting of the MSY exploitation rate is accompanied by high probabilities of the population crossing into the lower domain of stability. These high probabilities are dangerous if the exploitation rate is not reduced rapidly enough. For the case shown, the population succeeded in staying in the upper domain.

The nonlinear effect of environmental changes on the location of the boundary between the upper and lower domains of attraction is related to the slope of the recruitment curve near the intersections with the replacement line. The flatter the curve at these points relative to the replacement line, the greater is the change in the lower bound for a given change in the environmental factor (refer back to Fig. 9). Since higher values of parameter A of equation (1) result in steeper recruitment curves, enhanced salmon stocks, which may have higher A values, will have less uncertainty in the boundary locations than less productive stocks.

Because of this phenomenon, it might seem logical to desire all stock productivities to be boosted as high as possible within existing management constraints. However, this may not be the best option, as will be discussed in the next section, which deals with multiple-stock fisheries.

MULTIPLE STOCKS, DETERMINISTIC CASE

The approaches to the single-stock case are equally applicable to multiple-stock systems for investigating effects of different relative stock productivities on probability of stock collapse

(meaning a drastic drop to a much lower level, *though not necessarily to extinction*). It is assumed in the following analyses that there is no interaction between stocks and that exploitation rates are applied equally over all stocks.

Salmon fisheries where more than one stock is harvested simultaneously create special problems. If the stocks have very different productivities (A values in equation [1]) exploitation rates designed to optimally harvest the more productive stocks will increase the likelihood of overexploiting the less productive stocks (Ricker 1958a). One possible cause of this commonly recognized problem could be the dropping of the less productive stocks into their lower domains of stability. On the other hand, if stocks fished simultaneously have similar A values, then there is a lower chance of overharvesting the less productive stock.

What are the characteristics of multiple-stock salmon fisheries, and how similar should the A values ideally be? If depensatory mortality is at all common and significant in these fish, then we can use pairs of equations of the present model to investigate the relationships between similarities of stock productivities, their different MSY exploitation rates, and the amount of drop in sustainable catch if and when any stocks become overexploited. When enhancement is successfully carried out, the exploitation rates will presumably begin to increase, but to some unspecified level. It is this increasing exploitation rate which is the source of potential overexploitation problems.

Figure 12 shows the relationships between sustainable catch and exploitation rate for each of six pairs of stocks having different relative productivities. All stocks have parameter values as defined before in the Methods of Analysis section, except the most productive stock in all cases has $A = 2.0$ and the less productive stocks have A values ranging from 1.0 to 2.0 at intervals of 0.2. Several characteristics of these catch curves are important:

D = difference in exploitation rates causing the collapse of, first, the less productive stock (OEX_1) and then, the more productive stock (OEX_2).

R_p = ratio of productivities of the two stocks involved in the fishery, where $A_2 = 2.0$ and

$$R_p = A_1/A_2$$

CC_1 = cost of the collapse of the less productive stock of the pair, measured here strictly in terms of the decrease in sustainable catch below what it was just before overexploitation occurred.

CC_2 = same as CC_1, but for the more productive stock of the pair.

The curves in Fig. 12 illustrate several points. First, as is intuitively obvious, *the greater the*

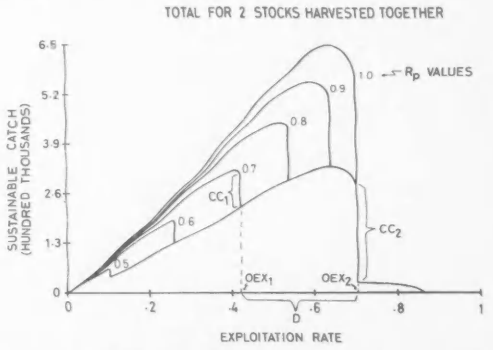

FIG. 12. The relation between exploitation rate and total sustainable catch from both stocks of different two-stock systems, each having different ratios of A values for their constituent stocks. See text for explanation of symbols.

similarity in productivities, the smaller is the difference between the exploitation rates that will cause each respective stock to drop into its lower domain of stability. On the other hand, if stock productivities are dissimilar, there might be more time to take corrective action on increasing exploitation rates before the most productive stock also becomes overexploited.

Second, the drop in sustainable catch owing to the collapse of the less productive stock (CC_1) increases as R_p approaches 1.0. When two stocks have similar productivities, the relatively large CC_1 acts as a strong warning signal, perhaps strong enough to stimulate the imposition of constraints on the developing fishery and to prevent the collapse of the second stock. But large feedback signals only occur when D is small. Thus, there is a trade-off. If the resolution of the monitoring system is such that practically all sizes of CC_1 are perceived as noise, then pairs of stocks with different R_p values will likely have little difference in the probability of overharvesting both stocks. Conversely, if good monitoring can detect a relatively small CC_1 as loss of a stock, then there will be great differences in chances of overexploiting both stocks between systems with different R_p values. The importance of generating and monitoring such feedback information is discussed by Holling (1969) and Walters and Hilborn (1976).

Finally the ratio CC_1/CC_2 increases with R_p, meaning that the loss of the less productive stock becomes more significant in terms of decreased sustainable catch when stocks have more similar A values. However, even if the probability of causing overexploitation of the second stock is low (D large), the cost of such a mistake is

nevertheless relatively large (i.e. the system may be more fail-safe, but the cost in the event of failure is high; Holling and Clark 1975). "Costs" as construed above imply "amount of disruption in the fishing industry" as well as lost profits or catch.

These results have interesting implications for one widely discussed plan for salmon enhancement in British Columbia, which is to bring many of the stocks fished simultaneously to about the same level of productivity, i.e. $R_p \simeq 1.0$ (Ricker 1975). This would certainly simplify management of these stocks, because then these stocks could sustain about the same maximum harvest rates. However, the situation is not simple. Increasing similarity in maximum harvest rates could increase the probability of causing a collapse of all stocks (by having decreased D), through a mistake in estimation of MSY or through variance in survival rates. The cost of such overexploitation (in terms of loss in catch) also increases with more similar A values. However, an attempt to retreat to the case of very dissimilar stock productivities will result in little feedback information being generated by loss of less productive stocks. Thus, the "best" mixture of stock productivities may be intermediate between the extremes of having all A values the same or having them quite diverse. Such an intermediate strategy would deliberately use the overexploitation of the less productive stock and the resulting drop in catch as a warning signal to control the developing fishery, and as feedback information to help determine boundaries of more productive stocks subject to the same predation. This approach perhaps seems inefficient because the less productive stock is made expendable to provide information about the total fishery complex. But this should be better than the situation where several stock productivities are identical and thus provide little feedback information until all stocks are overexploited more or less simultaneously. This point is particularly critical in salmon fisheries where, owing to their unusual nature, there is no precollapse shift in the age structure as there is in many long-lived species. One could even suggest that some salmon enhancement funds be set aside specifically for rehabilitation of these less productive stocks after they have generated feedback information.

The situation described above brings to mind the "Titanic Effect" (Watt 1974), which refers to the fact that the more improbable a disaster is, the more costly it will be when it inevitably happens because people will not have taken steps to minimize its impact. This attitude matches that of people who claim that enhanced salmon stocks having similar reproductive parameter values will not be overharvested simultaneously (because we have learned much from our past mistakes), and who therefore will help guarantee large costs of such inevitable mistakes. While the probability of such a catastrophic event occurring may be very small, it cannot be exactly zero; therefore, given enough time the event is by definition inevitable.

Application of the Concepts of Catastrophe Theory

We can view in another way how changes in catch, population sizes, and stability domains occur with changing exploitation rates by using the approach of catastrophe theory, which looks at rapid qualitative jumps from one set of equilibria to another (Thom 1975; Zeeman 1976). This theory has been only recently applied to ecological systems (Jones 1977; Jones and Walters 1976), but it has already proven its value in conceptualizing interactions among variables and controls in complex systems.

For the present examples of fish systems having depensatory mortality, we can calculate the equilibria of population size and catch that would result from a given exploitation rate. It is explicitly recognized that exploitation rates would never be held constant over several fish generations; however, the equilibrium calculated for each harvest rate would be the level toward which the population would tend to move in that generation. Figure 13 shows equilibrium population

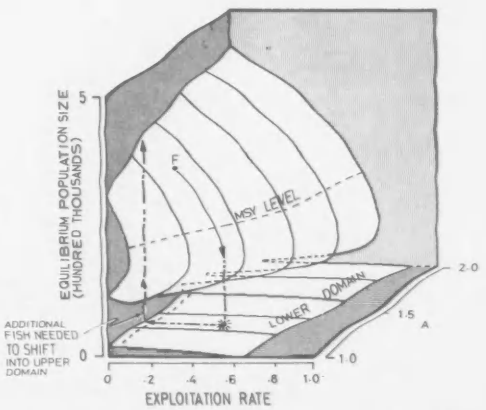

FIG. 13. Equilibrium population size for single stocks with A parameter values ranging from 1 to 2. For a given exploitation rate, there may be up to three equilibria, one stable in each of the upper and lower domains and one unstable (on the underside of the fold). These equilibria are the points A, B, and C of Fig. 1 (see text).

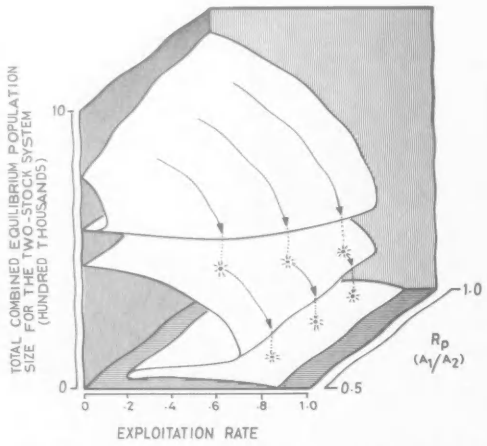

FIG. 14. Equilibria for different two-stock systems harvested simultaneously (see text). When the less productive stock of a given pair is overexploited, the system tends to drop toward the next stable equilibrium down on the surface below. Similarly, when the most productive stock is overharvested, the system drops into the lower domain.

sizes for several single stocks, each with an A value between 1.0 and 2.0. The total set of equilibrium points creates a surface called a manifold. The undersides of the folds are the unstable equilibria, so a population at any given A value and harvest rate will tend to move toward one of the stable equilibrium surfaces (see Jones 1977). For example, a fishery following a course described by the arrows on Fig. 13 would start at point F, and move along the manifold to near the MSY level of exploitation, at which point a slight increase in harvest rate might result in the population dropping to the lower domain. The exploitation could be relaxed on the stock and the population would slowly increase, but it would still be trapped in the lower domain. For a stock with this A value, it can be seen that even a zero harvest rate would not be sufficient for the stock to get pushed into the upper domain (whereas a 10% harvest rate would be sufficient for a stock with $A = 2.0$, because below that exploitation only the upper equilibria exist). Thus, the upper domain for the low A value stock could only be reached if environmental noise were great enough to move the population above the boundary between the two domains or if fish productivity were increased sufficiently, say, through enhancement.

Figure 14 shows the manifold of population size for pairs of stocks in a multistock fishery, with the same range of A values as shown in Fig. 12. The equilibria on the surfaces are total combined population sizes for the two-stock complex. When stocks have similar A values (R_p close to 1.0), there is a greater chance of overharvesting both simultaneously as discussed

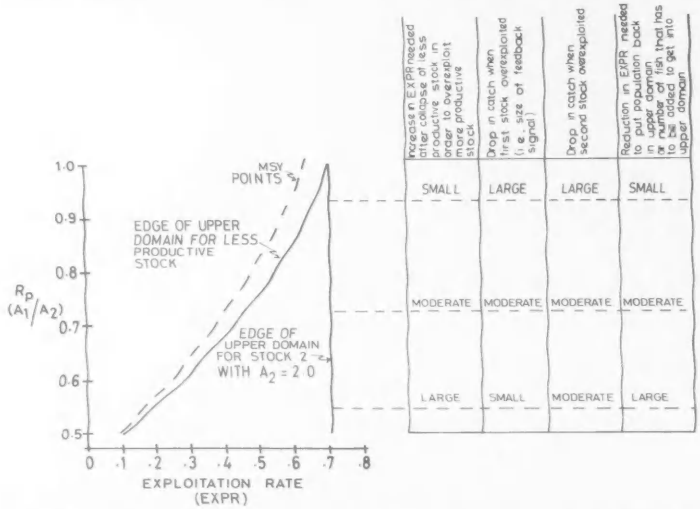
Increase in EXPR needed after loss of less productive stock in order to overexploit more productive stock
Drop in catch when first stock overexploited (i.e. size of feedback signal)
Drop in catch when second stock overexploited
Reduction in EXPR needed to put population back in upper domain in case where that has had to be added to get into upper domain
MSY POINTS
EDGE OF UPPER DOMAIN FOR LESS PRODUCTIVE STOCK
EDGE OF UPPER DOMAIN FOR STOCK 2 WITH $A_2 = 2.0$
SMALL LARGE LARGE SMALL
MODERATE MODERATE MODERATE MODERATE
LARGE SMALL MODERATE LARGE
1.0 0.9 0.8 0.7 0.6 0.5
R_p (A_1/A_2)
0 .1 .2 .3 .4 .5 .6 .7 .8
EXPLOITATION RATE (EXPR)

FIG. 15. When the drop-off points from the two upper folds in Fig. 14 are projected on to the R_p–EXPR plane, they trace these critical lines. As indicated, there would be different costs and benefits resulting from different values of R_p, which are taken here to represent different mixes of enhanced salmon stocks.

earlier. The edges of the manifold representing overexploitation points can be projected onto the R_p–EXPR plane as shown in Fig. 15. This figure summarizes the advantages and disadvantages of having R_p values close to 1.0, as discussed earlier. The similarity in stock productivity which is deemed best will depend on the relative importance of these various measures.

Conclusions

Since fish populations exposed to strong depensatory mortality processes may have two or more potential equilibria and associated domains of attraction, it is not reasonable to assume that populations can easily recover after being forced to low levels. However, this is the assumption of the Ricker stock–recruitment model which is used in management of many fisheries. Furthermore, sizes of domains of attraction change with exploitation rate and further problems are created by uncertain environmental conditions. The realization that more than one stability domain can exist should ideally result in more cautious management at high exploitation rates.

It may be possible to plot data for past stock collapses and rapid stock increases on an "A value vs. exploitation rate" plane to determine where the edges of the manifolds occur. Alternatively, one could try to measure the depensatory mortality processes such as predation to deduce an underlying model. In either case, this approach should help to define ways of boosting a population back into its upper domain. For example, one could determine how much the exploitation rate would need to be dropped, how many predators should be removed, how much to increase A, or how many fish should be added.

Finally, the general conclusions described here do not depend on the particular parameter values chosen for illustration. In fact, any population that has a significant depensatory mortality agent may potentially have the characteristics discussed above, which result from shrinking domains of stability as exploitation rate increases.

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Uptake and Clearance of Petroleum Hydrocarbons in the Ringed Seal, *Phoca hispida*

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Ringed seals, *Phoca hispida*, showed rapid absorption of hydrocarbons from Norman Wells crude oil into body tissues and fluids when exposed by both immersion and ingestion. Relatively low but significant levels were found in tissue, blood, and plasma. Levels in bile and urine were high, indicating these to be routes of excretion.

Key words: petroleum, hydrocarbons, benzene, ringed seal, immersion, ingestion, uptake, clearance

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Des phoques annelés, *Phoca hispida*, montrèrent une rapide absorption, dans les tissus et fluides corporels, d'hydrocarbures de pétrole brut de Norman Wells, lorsque exposés soit par immersion, soit par ingestion. Nous avons trouvé des concentrations relativement basses mais significatives dans le tissu, le sang et le plasma. Les concentrations dans la bile et l'urine sont élevées, démontrant qu'elles sont des voies d'excrétion.

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ASSOCIATED with the likelihood of extensive exploitation of arctic polar continental shelf oil reserves is a potential for spills because of the hazardous conditions of production and shipping in the arctic environment (Glaeser 1971). In addition, light crude oils such as found there, and as used in this study, have a high concentration of aromatic hydrocarbons with a low boiling point. These fractions have been shown to have marked toxicity in many organisms (Barnett and Kontogiannis 1975; Ottway 1971). At the low arctic temperatures, the toxic volatiles evaporate less readily and the effective toxicity of light crude oil is enhanced (Morrow 1973; Ottway 1971). A concise summary of oil toxicities is presented by Moore and Dwyer (1974).

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Little detailed information has been available on the extent of the effects of crude oil exposure in marine mammals. In seals, exposure has been cited to cause eye irritation (Nelson-Smith 1970) and other damage (California Department of Fish and Game 1969; Lillie 1954; Spooner 1967). The Santa Barbara channel oil spill has been suggested as the cause of mortalities in island colonies of california sea lions, *Zalophus californianus*, and northern elephant seals, *Mirounga leonina*. However, Brownell and *LeBoeuf* (1971) interpreted these as natural mortalities. LeBoeuf (1971) also reported that elephant seal pups recovered from oil coating. Reports of exposure of arctic seals to spilled oil show that no related mortalities occurred following contact (Hess and Trobaugh 1970; Morris 1970; Muller-Willie 1974).

Smith and Geraci (1975) and Geraci and

Smith (1976) reported behavioral, physiological, and pathological effects of crude oil in the ringed seal, *Phoca hispida*, as part of a comprehensive study of oil spills in the Beaufort Sea. In ringed seals, oil exposure by immersion resulted in transient problems of eye irritation, minor kidney damage, and possible liver lesions when carried out in the field, and in the death of the exposed animals when immersed in a laboratory study. No effects on body-core temperature were noted. Ingestion of the oil caused no significant lesions or behavioral changes. As part of that study, we assessed the uptake, distribution, and clearance of Norman Wells (N.W.T.) crude oil in ringed seals under conditions of surface contact by immersion and ingestion of contaminated fish.

Aside from the observable effects of oil exposure on seals, another consideration was that the indigenous peoples of the north, the Inuit in particular, use marine mammals, including the ringed seal, as food and for clothing and crafts. With such an involvement, cross contamination from seal to human must be considered but has been impossible to assess because there has been no qualitative nor quantitative information on petroleum hydrocarbon uptake following contamination in these marine mammals.

Materials and Methods

The oil immersion study was carried out on six seals, maintained in holding pens in seawater at the capture site, Brown's Harbour, on the east side of Cape Perry, N.W.T. (70°05′30″N, 124°22′30″W). The seals were immersed for 24 h in seawater covered by a 1-cm-thick layer of Norman Wells crude oil. Samples from the contaminant oil on the water surface were taken at 0, 1, 3, 6, 12, and 19 h for hydrocarbon analysis. After 24 h immersion, all six seals were transferred to clean seawater. Two seals were killed on day 2, three on day 6, and one on day 7 following their initial exposure to oil. A sample of muscle, kidney, blubber, brain, liver, lung, urine, bile, blood, and plasma was taken from each seal for hydrocarbon analysis. The samples were packaged airtight in aluminum foil or glass and stored frozen until analysis.

An ingestion study was carried out at Guelph on five ringed seals captured at Brown's Harbour. They were fed fish containing embedded gelatin capsules of Norman Wells crude at an oil dose of 5 ml/day for 5 consecutive days. The oil was labeled with ^{3}H-benzene to an activity of 1 mCi/5 ml. Blood, plasma, and biopsy samples of liver, blubber, and muscle were taken at frequent intervals during and for 28 days after the ingestion period. These samples were analyzed for tracer activity. Tissues and body fluids for controls for the ingestion, as well as the immersion study, were obtained from six ringed seals shot in open water near the camp and were assumed to be free of petroleum hydrocarbons. All details of capture, handling, and experimental design are given in Smith and Geraci (1975).

Aliquots of surface-slick oil samples taken during the oil immersion period were analyzed by gas chromatography on a support-coated open-tubular (SCOT) OV-1 column, temperature programmed at 4°/min from 60 to 275°C, and isothermal at 275°C. Aliquots of fresh Norman Wells crude oil were dissolved in hexane to characterize UV absorption and fluorescence spectra.

Extraction of petroleum from tissues and body fluids was carried out by steam distillation using the method of Ackman and Noble (1973). Characterization of petroleum hydrocarbons in the tissue and fluid distillates was carried out by UV absorption spectrophotometry. The extracts were scanned and compared with the absorption pattern of Norman Wells crude oil over a wavelength range of 190–350 nm.

Quantification of petroleum hydrocarbons in sample extracts was carried out by fluorometry, with excitation at 322 nm and fluorescence measurement at 365 nm using narrow band-pass filters. The choice of filters was based on a spectrofluorometric scan of the crude oil. The amount of fluorescence in an experimental sample significantly above that of the mean fluorescence of six control samples was interpreted to be due to Norman Wells crude oil fractions. Aliquots of crude oil were used as external standards for calibration of the extraction process and of the fluorometric analysis. The sensitivity of the analysis, expressed as petroleum hydrocarbon concentration in tissues or fluids (wet weight), was 0.5 μg/g.

Radiotracer analysis of tissues and fluids for ingested labeled petroleum hydrocarbons was by liquid scintillation counting, following the methods of Hansen and Busch (1967) and Anon. (1973). This included digestion of the sample with NCS solubilizer (Amersham/Searle), neutralization with glacial acetic acid, and, as required, bleaching with benzoyl peroxide.

Results and Discussion

Norman Wells crude oil showed peak absorption of the UV spectrum at 232 nm. The UV absorption peaks obtained from the fluids and tissues of the experimental seals coincided with those of Norman Wells crude oil. The fluorometric scan indicated a characteristic excitation peak at 325 nm and a fluorescence peak at 370 nm.

None of the tissues or fluids from the control animals showed any of the characteristic UV absorption peaks noted in the experimental samples. The control animals were then assumed to be free from petroleum contamination, at least within the limits of sensitivity of the method used. Background fluorescence of the control samples was interpreted to be due to native compounds.

The highest levels of hydrocarbons in the oil-immersed seals were found in the body fluids.

Urine and bile had the highest concentrations, 39 and 58 μg/g, respectively, 2 days after oiling. Urine levels declined with time, while bile concentrations remained high. Blood and plasma concentrations were much lower (Fig. 1), and both declined with time. Blubber, brain, muscle, kidney, and liver showed varying low concentrations of hydrocarbons with no significant pattern of change in concentration with time. Lung tissues showed only trace amounts in all seals, possibly indicating a very ready volatile loss once the animal was removed from the contaminant (Fig. 1).

Results from the ingestion study showed highest tracer activity in the blood on the 2nd day of dosing, with a sharp and continuing decline thereafter (Fig. 2). The absolute activity in plasma was somewhat lower but did not decline until after the end of the 5-day dosing period. All tissues taken by biopsy during the ingestion experiment showed pronounced activity in the day 2 sample (Table 1), liver and blubber more than muscle. All had less activity than blood and plasma taken at the same time. Liver and blubber activity declined to low levels by 28 days; muscle showed a less rapid decline.

Examination of weathered oil taken during 19 h after immersion of the seals in oil showed compositional changes, notably the losses of benzene and other low boiling point components,

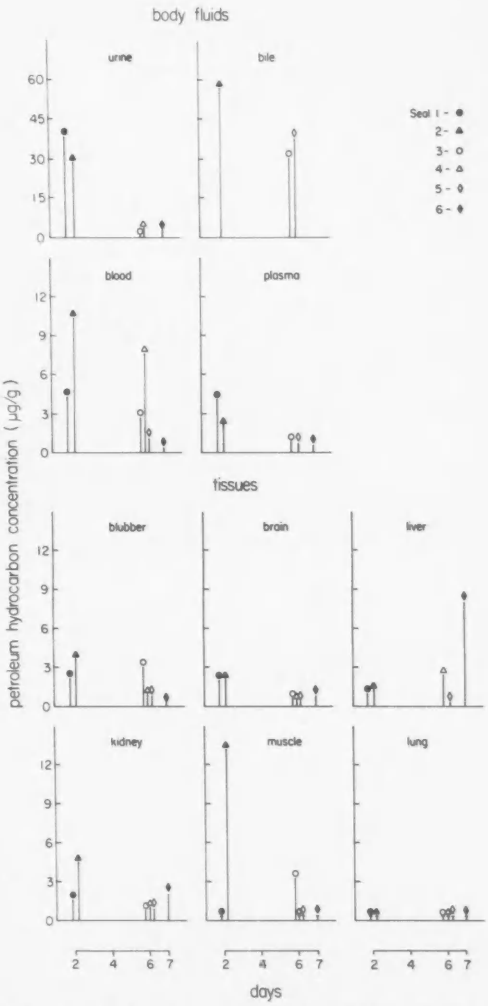

FIG. 1. Hydrocarbon concentrations determined by fluorometry in tissues and body fluids of six ringed seals, *Phoca hispida*, immersed in crude-oil-covered seawater.

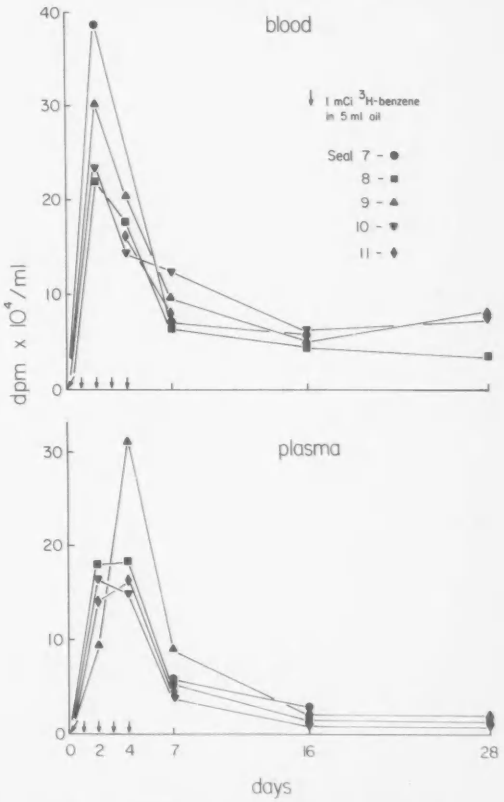

FIG. 2. Activity in ringed seal, *Phoca hispida*, blood and plasma following dietary ingestion of labeled crude oil, 1 mCi ^{3}H-benzene/5 ml oil per day for 5 consecutive days.

which are known to be acutely toxic (Moore and Dwyer 1974). Although most of these fractions were lost in a few hours, a high concentration of naphthalenic components remained. These are also toxic and are readily assimilated into tissues (Blumer et al. 1970; Stegman and Teal 1973). The process of aging and weathering of crude oils in and on seawater has been well documented by Boylan and Tripp (1971), Smith and MacIntyre (1971), Erhardt and Blumer (1972), Harrison et al. (1975), and many others.

The ringed seal apparently shows a rapid absorption of hydrocarbons from Norman Wells crude oil by both immersion and ingestion. In view of the fact that Smith and Geraci (1975) found no intestinal lesions nor presence of oil in the gut, it would seem that the uptake path by immersion was by way of skin or respiratory surface, or both. Lower accumulated levels of petroleum hydrocarbons in tissues than in bile and urine suggest biliary and renal routes of excretion. The latter site is supported by findings of renal tubular necrosis in at least one of the animals in this study. Although liver levels showed no obvious pattern of change over the 7-day period following immersion, there was a large decrease in liver hydrocarbons during the 3-wk period following oil ingestion. These differences may be due to a longer period of follow-up in the ingestion study or to the rapid dissipation of labeled benzene which was the only hydrocarbon specifically measured in that study. However, liver is regarded as a principal site of detoxification and excretion of lipophilic substances in many species (Hodgson 1974), and the present data suggest a similar function in the ringed seal. The amounts of hydrocarbons ingested did not cause obvious liver lesions in these studies, nor in harp seals given a much higher dose of crude oil (Geraci and Smith 1976). Unfortunately, no urine, bile, or postmortem tissue samples from the ingestion experiment could be analyzed.

This was an acute study. We have shown that brief contact with crude oil alone results in its accumulation in body fluids and tissues of a seal. Therefore, longer exposure would result in increased accumulation. The eventual concentration at which the detoxifying and excretory mechanisms would cease to function is unknown.

TABLE 1. Activity in ringed seal, *Phoca hispida*, tissue biopsies following dietary ingestion of labeled crude oil, 1 mCi ^{3}H-benzene/5 ml oil per day for 5 consecutive days.

Seal no.	Tissue	Activity (dpm × 10^4/g) 2 days	16 days	28 days
7	blubber	0.65	0.14	—
	liver	9.77	1.07	—
	muscle	2.42	0	—
8	blubber	7.60	0.33	0.09
	liver	7.06	0.66	0.08
	muscle	1.72	0.55	0.43
9	blubber	7.95	0.08	0
	liver	2.58	0.38	0.14
	muscle	1.79	0.24	0.18
10	blubber	2.19	0	0.02
	liver	5.57	0.43	0.64
	muscle	1.53	0.14	0.18
11	blubber	6.22	—	—
	liver	6.82	—	—
	muscle	1.68	—	—

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Evaluation of Tests with Early Life Stages of Fish for Predicting Long-Term Toxicity

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MCKIM, J. M. 1977. Evaluation of tests with early life stages of fish for predicting long-term toxicity. J. Fish. Res. Board Can. 34: 1148–1154.

Partial and complete life-cycle toxicity tests with fish, involving all developmental stages, have been used extensively in the establishment of water-quality criteria for aquatic life. During extended chronic exposures of fish to selected toxicants, certain developmental stages have frequently shown a greater sensitivity than others. In 56 life-cycle toxicity tests completed during the last decade with 34 organic and inorganic chemicals and four species of fish, the embryo–larval and early juvenile life stages were the most, or among the most, sensitive. Tests with these stages can be used to estimate the maximum acceptable toxicant concentration (MATC) within a factor of two in most cases. Therefore, toxicity tests with these early life stages of fish should be useful in establishing water-quality criteria and in screening large numbers of chemicals.

Key words: fish, embryos, larvae, chronic toxicity, early life stages

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On a fait un usage intensif d'essais de toxicité sur un cycle biologique partiel ou complet avec des poissons, et impliquant tous les stades de développement, afin d'établir des critères de qualité de l'eau pour la vie aquatique. Lors d'expositions chroniques prolongées de poissons à des toxiques choisis, certains stades de développement ont souvent montré une plus grande sensibilité que d'autres. Dans 56 essais de toxicité de tout un cycle biologique effectués durant la dernière décennie avec 34 substances chimiques organiques et inorganiques, et quatre espèces de poissons, les stades les plus sensibles, ou parmi les plus sensibles, ont été le stade embryon–larve et le début du stade juvénile. On peut faire des essais avec ces stades pour estimer la concentration toxique acceptable maximale (CTAM) dans les limites d'un ou de deux facteurs dans la plupart des cas. Les essais de toxicité sur les premiers stades de vie des poissons devraient donc être utiles dans l'établissement de critères de qualité de l'eau et dans l'évaluation d'un grand nombre de substances chimiques.

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THE life-cycle toxicity test with fish, involving all developmental stages, was proposed by Mount and Stephan (1967). In these early studies fathead minnows (*Pimephales promelas*) were exposed to a graded series of toxicant concentrations throughout the fish's life cycle, and the effects of the toxicant on survival, growth, and reproduction were measured quantitatively. These quantitative data allowed the determination of a maximum acceptable toxicant concentration (MATC), defined as the hypothetical toxic threshold concentration between the highest concentration tested having no observed effects and the next higher toxicant concentration having significant toxic effects (Mount and Stephan 1967).

Further development of life-cycle toxicity tests with other fish species followed. Eaton (1970) proposed the use of the bluegill (*Lepomis macrochirus*); McKim and Benoit (1971) developed methods for the brook trout (*Salvelinus fontinalis*); and Smith (1973) utilized the flagfish (*Jordanella floridae*) for life-cycle tests. For the last decade, life-cycle toxicity tests have provided the most reliable information on the long-term effects of toxic chemicals on fish and the basis for many of the established water-quality criteria for aquatic life.

During these extended life-cycle tests with several species of fish and a variety of toxicants, certain developmental stages have consistently shown a greater sensitivity than others. The possibility of focusing research efforts on these more sensitive stages holds considerable promise of success in the search for quicker and less costly ways of predicting the chronic toxicity of chemicals to fish. Several investigators have proposed predicting fish chronic toxicity through the use of

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shorter tests with early developmental stages of fish, which, with selected toxicants, were shown to be the most sensitive, or one of the most sensitive, parts of the life cycle (Pickering and Thatcher 1970; Pickering and Gast 1972; McKim et al. 1975; Eaton et al. 1977; McKim et al. 1977). These authors have emphasized that, with only a relatively short exposure of several months of the embryo–larval or early juvenile stages of fish to a toxicant, an estimate of the MATC can be made without carrying out the partial or complete life-cycle test.

This study reviews the available data from life-cycle toxicity tests with fish and evaluates (1) the hypothesis that the embryo–larval and early juvenile stages of development are among the most sensitive stages in life-cycle toxicity tests and (2) the usefulness of embryo–larval and early juvenile toxicity tests in estimating MATCs for fish exposed to individual and complex mixtures of chemicals.

Source of Data

The published and unpublished data from life-cycle toxicity tests with fish were reviewed. Partial and complete life-cycle toxicity studies were included, since a previous evaluation of life-cycle toxicity data by Andrew et al. (1977) indicated that partial life-cycle tests (juvenile through adult spawning to 3 mo after hatching of offspring) gave MATC values similar to complete life-cycle tests (embryos or newly hatched larvae through adult spawning to 3 mo after hatching of offspring). Only tests conducted according to specific methods recommended by the Committee on Aquatic Bioassays of the U.S. Environmental Protection Agency (1972) for fathead minnows (*Pimephales promelas*), bluegills (*Lepomis macrochirus*), brook trout (*Salvelinus fontinalis*), and flagfish (*Jordanella floridae*) were included in this evaluation. Deviations from these methods were allowed only if all developmental stages had been successfully tested and embryo–larval and early-juvenile exposures extended to a minimum of 30 days after hatching. The biological effects measured during all embryo–larval and early juvenile fish tests were decreases in hatchability, survival and growth, and increases in deformities.

The existing data were also examined to determine if offspring from unexposed parents (Pue) differed in their sensitivity to toxicants from offspring whose parents were exposed (Pe) and offspring whose parents' parents were exposed (Pe_1).

Results

Data from studies representing 34 toxicants and four fish species are presented in Table 1. In all of the 56 life-cycle tests judged acceptable for evaluation, the embryo–larval or early juvenile estimate of the MATC was within a factor of two of the actual MATC. In 46 (82%) of the tests the embryo–larval or early juvenile estimate of the MATC was essentially identical to the actual MATC. The endpoints in two of these tests (Table 1: test 22, trimetal mixture; 17, zinc) consisted of reduced adhesiveness of the egg and a fragility of the egg membrane, which was considered in the original papers as reduced egg production. Recent life-cycle tests with zinc and fathead minnows (Benoit and Holcombe, personal communication, Environmental Research Laboratory, Duluth, Minn.) showed that the number of eggs spawned was similar in all concentrations if fragile and loose eggs were counted. Therefore, the critical life stage in these earlier papers was considered here as embryo–larval.

Ten life-cycle tests of the total 56 (18%) showed that the embryo–larval or early juvenile estimate of the MATC would have deviated by a factor of two or less from the actual MATC. One of the 10, which initially did not indicate the embryo–larval and early juvenile stages to be the most sensitive, was repeated 3 times, and in each case these early stages were the most sensitive (Table 1: tests 3, 4, 5, and 6, cadmium). In the other nine life-cycle tests (Table 1: test 15, lead; 18 and 19, zinc; 23, methylmercury; 27, chloramine; 33, atrazine; 41, lindane; 46, trifluralin; and 40, Guthion®) the early developmental stages were not among the most sensitive. However, the deviation was again only a factor of two, and in five of these cases (Table 1: tests 15, 18, 19, 23, and 27) other species were tested with the same or very similar compounds and showed the embryo–larval and early juvenile stages were again the most sensitive. The MATCs for a specific toxicant, species, and water combination sometimes vary by a factor of two. For example, flagfish exposed to cadmium in soft water (Table 1: tests 3, 4, 5, and 6) and flagfish exposed to zinc in soft water (Table 1: tests 18 and 19) emphasize this point.

Embryos and larvae from exposed parents were used in all 56 life-cycle toxicity tests evaluated in Table 1, but offspring from both unexposed and exposed parents were used in only 29 tests. In 23 of these tests (79%) no difference in sensitivity between embryos and larvae from previously exposed and unexposed parents was observed (see asterisks, Table 1). The two zinc life-cycle tests mentioned earlier (Table 1: tests 17 and 22) were not included in this evaluation because the embryos (Pue) were exposed after water hardening, and later work (Benoit and Holcombe, personal communication, Environmental Research Laboratory, Duluth, Minnesota) has indicated that zinc

TABLE 1. Results of partial (P) and complete (C) life-cycle toxicity tests with fish including the maximum acceptable toxicant concentration (MATC) established by each life-cycle test and an MATC estimated by embryo–larval and early juvenile (ELEJ) exposures conducted as part of each life-cycle test. Pue, embryos and larvae from previously unexposed parents; Pe from previously exposed parents; Pe_1, from previously exposed first-generation parents. A, adult; M, mortality; G, growth; F, egg fragility; H, hatchability; D, deformities; S, spawning. *No difference in sensitivity between embryos and larvae from previously exposed (Pe) and unexposed (Pue) parents.

Toxicant	Species	Type of life-cycle test	Critical life stage and effects	MATC (μg/ℓ)	Estimated MATC (μg/ℓ)	Type of embryo-larval test (days)	Reference
Metals							
1. Cadmium	Fathead minnow	P	ELEJ-H	37.0–57.0	37.0–57.0	*60 (Pue) (Pe)	Pickering and Gast (1972)
2. Cadmium	Bluegill	P	ELEJ-M,G	31.0–80.0	31.0–80.0	60 (Pe)	Eaton (1974)
3. Cadmium	Flagfish	C	A-S	4.1–8.1	8.1–16.0	60 (Pue)	Spehar (1976)
4. Cadmium	Flagfish	C	ELEJ-M	7.4–16.9	7.4–16.9	*30 (Pue) (Pe)	Carlson and Tucker[a]
5. Cadmium	Flagfish	C	ELEJ-M	3.0–6.5	3.0–6.5	30 (Pue) (Pe)	Carlson and Tucker[a]
6. Cadmium	Flagfish	C	ELEJ-M	3.4–7.3	3.4–7.3	30 (Pue) (Pe)	Carlson and Tucker[a]
7. Cadmium	Brook trout	C	ELEJ-G	1.7–3.4	1.7–3.4	90 (Pe) (Pe_1)	Benoit et al. (1976)
8. Copper	Fathead minnow	P	ELEJ-M; A-S	10.6–18.4	10.6–18.4	*120 (Pue) (Pe)	Mount and Stephan (1969)
9. Copper	Brook trout	P	ELEJ-G	9.5–17.4	9.5–17.4	90 (Pe)	McKim and Benoit (1971)
10. Copper	Brook trout	C	ELEJ-G	9.5–17.4	9.5–17.4	*90 (Pue) (Pe) (Pe_1)	McKim and Benoit (1974)
11. Copper	Bluegill	P	ELEJ-M	21.0–40.0	21.0–40.0	90 (Pue)	Benoit (1975)
12. Chromium	Fathead minnow	P	ELEJ-M,G	1,000.0–3,950.0	1,000.0–3,950.0	30 (Pue)	Pickering[a]
13. Chromium	Brook trout	C	ELEJ-M	200.0–350.0	200.0–350.0	*90 (Pue) (Pe)	Benoit (1976)
14. Lead	Brook trout	C	ELEJ-D	58.0–119.0	58.0–119.0	120 (Pe) (Pe_1)	Holcombe et al. (1976)
15. Lead	Flagfish	C	A-S	31.3–62.5	62.5–125.0	*120 (Pue) (Pe)	Anderson[a]
16. Nickel	Fathead minnow	P	ELEJ-H	380.0–730.0	380.0–730.0	30 (Pe)	Pickering (1974)
17. Zinc	Fathead minnow	P	ELEJ-F	30.0–180.0	30.0–180.0	30 (Pe)	Brungs (1969)
18. Zinc	Flagfish	C	A-G	26.0–51.0	51.0–85.0	30 (Pue)	Spehar (1976)
19. Zinc	Flagfish	C	A-G	75.0–139.0	139.0–267.0	30 (Pue)	Spehar (1976)
20. Zinc	Brook trout	P	ELEJ-F	532.0–1,368.0	532.0–1,368.0	*90 (Pue) (Pe) (Pe_1)	Holcombe and Benoit[a]
21. Zinc	Fathead minnow	C	ELEJ-F	78.0–145.0	78.0–145.0	*90 (Pue) (Pe)	Benoit and Holcombe[a]
Tri-metal							
22. Mixture	Fathead minnow	P	ELEJ-F			30 (Pe)	Eaton (1973)
Zinc +				27.3–42.3	27.3–42.3		
Cadmium +				3.9–7.1	3.9–7.1		
Copper				5.3–6.7	5.3–6.7		
Organo-metallics							
23. Methylmercury	Fathead minnow	C	A-M,S	0.07–0.13	0.13–0.23	60 (Pue)	Mount and Olson[a]
24. Methylmercury	Flagfish	P	ELEJ-G; A-S	0.17–0.33	0.17–0.33	30 (Pue)	Smith[a]
25. Methylmercury	Brook trout	C	ELEJ-M,G	0.29–0.93	0.29–0.93	90 (Pe) (Pe_1)	McKim et al. (1976)
Halogens							
26. Chlorine	Fathead minnow	P	ELEJ-M	14.0–42.0	14.0–42.0	60 (Pe)	Arthur et al. (1975)
27. Chloramine	Fathead minnow	P	A-S	16.0–43.0	43.0–108.0	30 (Pe)	Arthur and Eaton (1971)
28. Fluoride	Fathead minnow	P	ELEJ-M	6,800.0–13,600.0	6,800.0–13,600.0	30 (Pe)	Olson[a]
PCBs							
29. PCB-1254	Fathead minnow	C	ELEJ-M	1.8–4.6	1.8–4.6	*90 (Pue) (Pe)	Nebeker et al. (1974)
30. PCB-1242	Fathead minnow	C	ELEJ-M	5.4–15.0	5.4–15.0	*90 (Pue) (Pe)	Nebeker et al. (1974)
31. PCB-1248	Fathead minnow	C	ELEJ-M	1.1–3.0	1.1–4.4	*60 (Pue) (Pe)	DeFoe et al. (1977)
32. PCB-1260	Fathead minnow	C	ELEJ-M	2.1–4.0	2.1–4.0	*60 (Pue) (Pe)	DeFoe et al. (1977)
Pesticides							
33. Atrazine	Brook trout	P	A-G	60.0–120.0	120.0–240.0	*90 (Pue) (Pe)	Macek et al. (1976b)
34. Captan	Fathead minnow	P	ELEJ-M,G	16.5–39.5	16.5–39.5	30 (Pe)	Hermanutz et al. (1973)
35. Carbaryl	Fathead minnow	C	ELEJ-M	210.0–680.0	210.0–680.0	*60 (Pue) (Pe)	Carlson (1971)
36. Diazinon	Flagfish	C	ELEJ-H	54.0–88.0	54.0–88.0	*60 (Pue) (Pe)	Allison (1977)
37. Diazinon	Fathead minnow	P	ELEJ-M,G	6.8–13.5	6.8–13.5	60 (Pue) (Pe)	Allison and Hermanutz (1977)
38. Diazinon	Brook trout	P	ELEJ-G	<0.80	<0.80	120 (Pue) (Pe)	Allison and Hermanutz (1977)
39. Endrin	Flagfish	C	ELEJ-G	0.22–0.30	0.22–0.30	30 (Pue) (Pe)	Hermanutz (1977)
40. Guthion®	Fathead minnow	C	A-S	0.33–0.51	0.7–1.8[b]	*50 (Pue) (Pe)	Adelman et al. (1976)
41. Lindane	Fathead minnow	C	A-G	9.1–34.5	No effect	60 (Pe)	Macek et al. (1976a)
42. Malathion	Flagfish	C	ELEJ-G	8.6–10.9	8.6–10.9	30 (Pue) (Pe)	Hermanutz (1977)
43. Acrolein	Fathead minnow	P	ELEJ-M	11.4–41.7	11.4–41.7	30 (Pe)	Macek et al. (1976c)
44. Heptachlor	Fathead minnow	C	ELEJ-M	0.86–1.84	0.86–1.84	*60 (Pue) (Pe)	Macek et al. (1976c)
45. Endosulfan	Fathead minnow	P	ELEJ-H	0.20–0.40	0.20–0.40	30 (Pue)	Macek et al. (1976c)
46. Trifluralin	Fathead minnow	P	A-M	1.95–5.1	5.1–8.2	60 (Pe)	Macek et al. (1976c)
47. Toxaphene	Brook trout	P	ELEJ-M,G	<0.039	<0.039	60 (Pue)	Mayer et al. (1975)

TABLE 1. (*Concluded*)

Toxicant	Species	Type of life-cycle test	Critical life stage and effects	MATC (μg/ℓ)	Estimated MATC (μg/ℓ)	Type of embryo-larval test (days)	Reference
Sewage							
48. Nondisinfected	Fathead minnow	C	ELEJ-M,G	25–50%	25–50%	*30 (Pue) (Pe)	Ward et al. (1976)
49. Chlorinated	Fathead minnow	C	ELEJ-G	7–14%	7–14%	*30 (Pue) (Pe)	Ward et al. (1976)
50. Dechlorinated	Fathead minnow	C	ELEJ-M	50–100%	50–100%	*30 (Pue) (Pe)	Ward et al. (1976)
51. Chlorobrominated	Fathead minnow	C	ELEJ-M	50–100%	50–100%	*30 (Pue) (Pe)	Ward et al. (1976)
Other							
52. Linear alkylate sulfonate	Fathead minnow	P	ELEJ-M	630.0–1,200.0	630.0–1,200.0	30 (Pe)	Pickering and Thatcher (1970)
53. pH	Fathead minnow	C	ELEJ-H	6.6–5.9 (pH)	6.6–5.9 (pH)	*30 (Pue) (Pe)	Mount (1973)
54. pH	Brook trout	P	ELEJ-M,G	6.5–6.1 (pH)	6.5–6.1 (pH)	*90 (Pue) (Pe)	Menendez (1976)
55. NTA	Fathead minnow	P	A-M	54,000.0–114,000.0	54,000.0–114,000.0	—	Arthur et al. (1974)
56. Oxygen	Fathead minnow	P	ELEJ-M	5.01–4.02 (mg/ℓ)	5.01–4.02 (mg/ℓ)	30 (Pe)	Brungs (1971)

[a]Personal communication, Environmental Research Laboratory, Duluth, Minn.
[b]Author states value may be high by 50%.

effects show up only when the embryos are exposed before water hardening of the eggs.

In six of the tests (21%) embryos and larvae from exposed and unexposed parents differed in sensitivity, but never by more than a factor of three. In two of these tests (tests 5 and 6, cadmium) the embryos from exposed parents were more sensitive than those from unexposed parents. In contrast, in a third cadmium test (test 4) run simultaneously with the first two, embryos, larvae, and early juveniles from unexposed and exposed parents did not differ in sensitivity. In other tests with organics (test 38, endrin; 40, malathion), the embryos and larvae of unexposed parents appeared to be more sensitive than those of exposed parents. However, the greater variability in effects between concentrations in the experiment with embryos from exposed parents may have masked the significant effects observed in offspring from unexposed parents. Opposite results were seen with diazinon (tests 37 and 38), where embryos and larvae from unexposed parents seemed to be less sensitive than those from exposed parents. However, in a third diazinon test (test 36) flagfish embryos and larvae from unexposed and exposed parents did not differ in sensitivity.

Embryos and larvae from second-generation exposed parents (Pe_1) were also used in embryo–larval and early juvenile toxicity tests, and their sensitivity was compared with that of their parents (Pe) (Table 1: test 7, cadmium; 10, copper; 14, lead; 20, zinc; 25, methylmercury). Differences in sensitivity were not great enough to alter the MATC values generated by the two groups of offspring.

Thus, in more than half of the 56 life-cycle tests reported in Table 1, the sensitivity of embryo–larval or early juvenile fish from exposed and unexposed parents was usually the same, and in only two tests (37 and 38, diazinon) did it differ by a factor greater than two.

Discussion

Data on 56 life-cycle toxicity tests with four species of fish completed during the last decade with 34 different organic and inorganic chemicals, showed the embryo–larval and early juvenile life stages were the most, or among the most, sensitive in life-cycle tests. Toxicity tests with these stages can be used to estimate the MATC within a factor of two in most cases. Eight-two percent of the time the MATC estimated by embryo–larval or early juvenile exposures was identical to the MATC established by the longer, more involved, and more costly partial or complete life-cycle

TABLE 2. Estimated maximum acceptable toxicant concentration (MATC) for 12 species of fish established by embryo–larval and early juvenile tests and grouped according to the quality of diluent water used.

Water type and test location	Species	Estimated MATC (μg/ℓ)	Type of embryo–larval test	Reference
		Cadmium		
Soft water (45 mg/ℓ as $CaCO_3$) Duluth, Minn.	Flagfish	8.1–16.0	60-day (Pue) 25°C	Spehar (1976)
	Flagfish	7.4–16.9	30-day (Pue) (Pe) 25°C	Carlson and Tucker[a]
	Flagfish	3.0–6.5	30-day (Pue) (Pe) 25°C	Carlson and Tucker[a]
	Flagfish	3.4–7.3	30-day (Pue) (Pe) 25°C	Carlson and Tucker[a]
	Brook trout	1.7–3.4	90-day (Pe) 9°C	Benoit et al. (1976)
	Brook trout	1.1–3.8	90-day (Pue) 10°C	Eaton et al. (1977)
	Brown trout	3.8–11.7	60-day (Pue) 10°C	Eaton et al. (1977)
	Lake trout	4.4–12.3	60-day (Pue) 10°C	Eaton et al. (1977)
	Coho salmon	4.1–12.5	60-day (Pue) 10°C	Eaton et al. (1977)
	Northern pike	4.0–12.9	30-day (Pue) 16°C	Eaton et al. (1977)
	Smallmouth bass	4.3–12.7	30-day (Pue) 20°C	Eaton et al. (1977)
	White sucker	4.2–12.0	30-day (Pue) 18°C	Eaton et al. (1977)
Soft water (36 mg/ℓ as $CaCO_3$) Wareham, Mass.	Brook trout	1.0–3.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Channel catfish	11.0–17.0	60-day (Pue) 22°C	Sauter et al. (1977)
Hard water (200 mg/ℓ as $CaCO_3$) Newtown, Ohio	Fathead minnow	37.0–57.0	60-day (Pue) (Pe) 24°C	Pickering and Gast (1972)
	Bluegill	31.0–80.0	60-day (Pe) 26°C	Eaton (1974)
Hard water (187 mg/ℓ as $CaCO_3$) Wareham, Mass.	Brook trout	7.0–12.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Channel catfish	12.0–17.0	60-day (Pue) 22°C	Sauter et al. (1977)
		Chromium		
Soft water (36 mg/ℓ as $CaCO_3$) Wareham, Mass.	Rainbow trout	51.0–105.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Lake trout	105.0–194.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Channel catfish	150.0–305.0	60-day (Pue) 22°C	Sauter et al. (1977)
	Bluegill	522.0–1,122.0	60-day (Pue) 25°C	Sauter et al. (1977)
	White sucker	290.0–538.0	60-day (Pue) 17°C	Sauter et al. (1977)
Soft water (45 mg/ℓ as $CaCO_3$) Duluth, Minn.	Rainbow trout	200.0–350.0	90-day (Pue) 10°C	Benoit (1976)
	Brook trout	200.0–350.0	90-day (Pue) 9°C	Benoit (1976)
		Copper		
Soft water (40 mg/ℓ as $CaCO_3$) Newtown, Ohio	Fathead minnows	10.6–18.4	90-day (Pue) (Pe) 24°C	Mount and Stephan (1969)
Soft water (45 mg/ℓ as $CaCO_3$) Duluth, Minn.	Brook trout	9.5–17.4	90-day (Pe) 9°C	McKim and Benoit (1971)
	Brown trout	9.5–17.4	90-day (Pue) (Pe) 9°C	McKim and Benoit (1974)
	Bluegill	21.0–40.0	90-day (Pue) 27°C	Benoit (1975)
	Brook trout	22.3–43.5	60-day (Pue) 6°C	McKim et al. (1977)
	Lake trout	22.0–42.3	60-day (Pue) 6°C	McKim et al. (1977)
	Brown trout	22.0–43.2	60-day (Pue) 6°C	McKim et al. (1977)
	Rainbow trout	11.4–31.7	30-day (Pue) 11°C	McKim et al. (1977)
	White sucker	12.9–33.8	30-day (Pue) 15°C	McKim et al. (1977)
	Northern pike	34.9–104.4	30-day (Pue) 16°C	McKim et al. (1977)
Soft water (36 mg/ℓ as $CaCO_3$) Wareham, Mass.	Brook trout	5.0–7.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Channel catfish	12.0–18.0	60-day (Pue) 22°C	Sauter et al. (1977)
Hard water (187 mg/ℓ as $CaCO_3$) Wareham, Mass.	Brook trout	5.0–8.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Channel catfish	13.0–19.0	60-day (Pue) 22°C	Sauter et al. (1977)
		Lead		
Soft water (45 mg/ℓ as $CaCO_3$) Duluth, Minn.	Brook trout	58.0–119.0	(Pe) 9°C	Holcombe et al. (1976)
	Flagfish	60.0–125.0	(Pue) 27°C	Anderson et al.[a]
Soft water (36 mg/ℓ as $CaCO_3$) Wareham, Mass.	Rainbow trout	71.0–146.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Lake trout	48.0–83.0	60-day (Pue) 10°C	Sauter et al. (1977)
	Channel catfish	75.0–136.0	60-day (Pue) 22°C	Sauter et al. (1977)
	Blugill	70.0–120.0	60-day (Pue) 25°C	Sauter et al. (1977)
	White sucker	119.0–253.0	60-day (Pue) 17°C	Sauter et al. (1977)
		Zinc		
Soft water (45 mg/ℓ as $CaCO_3$) Duluth, Minn.	Flagfish	51.0–85.0	30-day (Pue) 25°C	Spehar (1976)
	Flagfish	139.0–267.0	30-day (Pue) 25°C	Spehar (1976)
	Brook trout	532.0–1,368.0	90-day (Pue) (Pe) 9°C	Holcombe and Benoit[a]
	Fathead minnow	78.0–145.0	90-day (Pue) (Pe) 23°C	Benoit and Holcombe[a]
		Organo–metallics methylmercuric chloride		
Soft water (45 mg/ℓ as $CaCO_3$) Duluth, Minn.	Fathead minnow	0.13–0.23	60-day (Pue) 23°C	Mount and Olson[a]
	Flagfish	0.17–0.33	30-day (Pue) 25°C	Smith[a]
	Brook trout	0.29–0.93	90-day (Pe) 9°C	McKim et al. (1976)
		Linear alkylate sulfate (LAS)		
Soft water (45 mg/ℓ as $CaCO_3$) Duluth, Minn.	Fathead minnow	1,100.0	30-day (Pue) 23°C	McKim et al. (1975)
	Northern pike	1,200.0	30-day (Pue) 15°C	McKim et al. (1975)
	Smallmouth bass	5,800.0	30-day (Pue) 15°C	McKim et al. (1975)
	White sucker	500.0	30-day (Pue) 15°C	McKim et al. (1975)

[a]Personal communication, Environmental Research Laboratory, Duluth, Minn.

toxicity test. Water quality, species, type of toxicant, and parental exposure had little effect on these conclusions.

If the above is true for individual toxicants, it should also be true of toxicant mixtures or complex effluents. Little information is available on life-cycle toxicity tests with complex effluents or mixtures, but the work cited in Table 1 on sewage (tests 49–51) and metal mixtures (test 22) supports this assumption to some degree.

Data on the sensitivity of various species to a single toxicant in the same water have been summarized in Table 2. With some toxicants species differences in sensitivity were not very great, yet with other toxicants sensitivity varied considerably among species. Thus the most important species or the most sensitive, if known, should be tested in any given situation. For screening large numbers of chemicals the use of one or two consistently sensitive species (e.g. fathead minnows) would probably suffice until more is known about species sensitivity to specific types or classes of compounds.

An estimate of the MATC based on tests with early life stages could be used with the 96-h LC50 to produce an application factor (AF = estimated MATC/LC50), similar to that defined by Mount and Stephan (1967) (AF = MATC/LC50) for use in extrapolating to other situations. However, the validity of such a relationship would have to be examined (Andrew et al. 1977).

Laboratory methods are now available for embryo–larval tests that would allow the relatively rapid screening of chemicals with selected species. Further development of these tests for the laboratory and for on-site (field) testing is under way, with the major emphasis on reducing the duration of exposure.

Muul et al. (1976) described the need in mammalian toxicology for more rapid, less costly tests to screen out potentially carcinogenic and toxic chemicals from the ever-expanding list of potentially useful chemicals. Faster, less costly testing procedures are also of extreme importance in aquatic toxicology, and in the USA this is especially so with the implementation of the Federal Environmental Pesticide Control Act of 1972 and the Toxic Substances Control Act of 1976, both of which will require prescreening by industry of some chemicals before commercial production. The use of embryo–larval fish toxicity tests would make possible the screening of large numbers of chemicals rapidly at a far lower cost per test than a partial or complete life-cycle toxicity test.

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I commend those researchers who, through their devoted efforts over the last decade, have made these data on chronic fish toxicity available to aquatic toxicologists. I also thank those researchers at the Environmental Research Laboratory, Duluth, Minn., who made their unpublished data available for inclusion in this evaluation and critically reviewed the paper.

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A Stochastic Model for the Management of the Northwestern Atlantic Harp Seal (*Pagophilus groenlandicus*) Population

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LETT, P. F., AND T. BENJAMINSEN. 1977. A stochastic model for the management of the northwestern Atlantic harp seal (*Pagophilus groenlandicus*) population. J. Fish. Res. Board Can. 34: 1155–1187.

Advice from the scientific advisers under the auspices of ICNAF to the international commissioners for 1977 was that the total allowable catch (TAC) for harp seals (*Pagophilus groenlandicus*) should not exceed 170,000. This advice, in part, was based on the scientific arguments presented in this paper. A stochastic model is developed that takes into account the variations in natural mortality and the landsmen's high arctic and Greenland catches. The Canadian–Norwegian large vessel hunt is controlled under quota regulations. The model is nonlinear, a result of changes in fertility and fecundity rates in response to shifts in population size. The maximum sustainable yield (MSY) 1+ population size is determined to be 1.6 million seals, or a breeding stock size of 375,000 seals. The MSY is approximately 240,000 seals assuming the hunt continues its present pattern. The 240,000 can further be split into 200,000 pups and 40,000 1+ seals. Present stock size is approximately 1.2 million and a TAC of 170,000 seals will allow the population size to reach to MSY level in 10–15 yr. A number of other management strategies are considered, in addition to prospects for future research.

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Selon les conseils fournis aux commissaires internationaux par les aviseurs scientifiques sous les auspices de l'ICNAF, les prises totales admissibles, PTA, de phoques du Groenland (*Pagophilus groenlandicus*) ne devraient pas dépasser 170 000 en 1977. Cette opinion est fondée en partie sur les arguments scientifiques présentés dans cet article. On élabore un modèle stochastique qui tient compte des variations dans la mortalité naturelle et des prises des chasseurs de terre du Haut-Arctique et du Groenland. La chasse par les grands navires canadiens–norvégiens est contrôlée par des contingents réglementaires. Le modèle est non linéaire, résultat des changements dans la fécondité en réponse à des changements dans la taille de la population. Le rendement maximum soutenable, RMS, taille de la population de 1+, est évalué à 1.6 million de phoques, ou un stock reproducteur de 375 000 phoques. Le RMS est d'environ 240 000 phoques, à supposer que la chasse se poursuive suivant les mêmes modalités. On peut de plus subdiviser le 240 000 en 200 000 chiots et 40 000 phoques de 1+. La taille du stock actuel est approximativement 1.2 million et des PTA de 170 000 phoques permettront à la population d'atteindre le niveau du RMS en 10–15 ans. On examine un certain nombre d'autres stratégies de gestion, en plus de perspectives de recherche future.

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THE exploitation of the northwestern Atlantic harp seal (*Pagophilus groenlandicus*) has been well documented, especially in recent years. Nearly 10 million harp seals are known to have been harvested from this population between 1895 and 1946 (Fisher 1955) and another 5.3 million were taken between 1947 and 1964 (Øritsland 1967). From 1965 to 1974, another 2.3 million seals were slaughtered in the northwestern Atlantic. This gives an average minimum annual kill, due to unreported catch, of 220,000

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seals over the period, a figure which has sustained the fishery for 80 yr. Recent regulations have set a quota for seals at 150,000 animals between 1972 and 1975 (ICNAF 1972), with a low quota restriction in 1976 permitting the take of only 127,000 seals. These quotas do not include the high arctic or Greenland catches, which can be considered to be approximately 10,000 animals. However, despite the low quota for 1976, 174,000[1] seals were killed.

Conflicting views as to the present status of the northwestern Atlantic harp seal have recently generated much controversy. These divergent opinions resulted from the interpretation of incomplete data sets and poor communication among participating scientists. However, there are methods such as ultraviolet aerial sensing, which can be used independent of supportive biological information, and do not rely on any subjective, current scientific opinion. Unfortunately, to date this method produces a "best estimate" of pup production in 1975 which is approximately 15,000 animals less than the catch (Lavigne et al. 1975).

Due to large discrepancies in estimation of production and natural mortality, it has been necessary to revise the basic data to incorporate the effects of the diverse fisheries and, in addition, to use statistical and computer techniques to assess the data, thus producing a reliable assessment of the northwestern Atlantic harp seal stock.

Materials and Methods

The assessment of an animal population requires the estimation of certain vital rates. Estimation of these rates, to a large extent, consists of analyzing age frequencies that represent either the population or the catch structure. In some populations the catch and population age structures are assumed synonymous; however, this assumption can lead to grave errors in the instance of the northwestern Atlantic harp seal population (Benjaminsen and Øritsland 1975).

Initially, the problem consists of producing an age frequency of the total annual catch for 1-yr-old and older seals (1+), which amalgamates the catch frequencies from the individual fisheries in their proper proportions. In this fishery the age distribution for the different fisheries is indeed diverse.

Shot samples from Notre Dame Bay, Newfoundland, consist primarily of seals that have not fully developed their mature markings, known as bedlamers. The La Tabatière, Quebec, and Labrador net fisheries usually result in a sample with a preponderance of mature animals, while the St. Anthony, Newfoundland, shot samples seem to be more representative of the population structure. On average each of these fisheries tends to be roughly equivalent in overall catch and can be summed to represent the landsmen's catch without producing serious errors. The large ships' catch from the molting patches, however, is quite different in structure from the overall landsmen's and must be treated separately. One of the primary problems is the fraction of 1-yr-old seals in the sample. This age-group is usually segregated from the remaining age-groups and is only randomly encountered when the molting patch is sampled (Benjaminsen and Øritsland 1975). Furthermore, the closing date also affects the large vessel sample; the earlier the hunt in the molting patches is terminated, the fewer females are represented in the catch (Sergeant 1965; Øritsland 1971). Thus, the mature composite age frequencies vary depending on the length of the hunt, and consist mainly of males (Fig. 1). In addition, the fraction of males present as bedlamers depends on the fraction mature in relation to their age. Samples of the Greenland and the high arctic hunt, representing 8% of the total catch on average, are excluded from this analysis from 1952 to 1975 since no consistent sampling and catch records are available.

Between 1952 and 1960, jaws were collected on a regular basis from the landsmen's catch and this sector of the hunt can be considered to be well represented (Sergeant and Fisher 1960; Sergeant personal communication) (Table 1). During 1952–54 and 1957–58 samples were also collected from the large vessels. However, the 1957–58 samples are sparse and it is unlikely that they accurately represent the catch. For this reason the years 1955–60 were replaced by an average catch frequency for large vessels. The attendant errors are possibly serious since during this period the large vessel hunt on 1+ animals represented between 87.5 and 95.5% of the total catch (Table 2).

In 1961 sampling began to steadily improve with both the large vessel catch from the molting lairs and the landsmen's catch being well represented (Table 1). Annual catch-at-age samples from 1961 on came from a number of sources (Sergeant 1971, 1972, personal communication; Øritsland 1971; Benjamin-

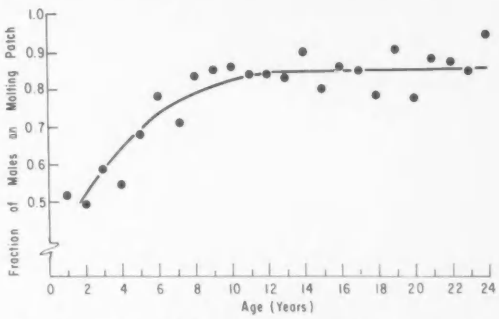

FIG. 1. The fraction of males in the Norwegian catch of molting northwest Atlantic harp seals (*Pagophilus groenlandicus*) from 1969 to 1974 (from Benjaminsen and Øritsland 1975).

[1]This number is subject to slight alterations.

sen and Øritsland 1975). Unfortunately, there was not a good sample taken for either the landsmen's or the large vessel catch in 1972, but the available data were included in the ensuing analysis. In 1973 the landsmen's sample was again lacking and may not sufficiently represent the fishery. In both 1972 and 1973 there was no basis for using an average sample to represent either fishery, especially since the landsmen's and large vessel catches are nearly equivalent to each other. In general, the samples from large vessels seemed to improve from 1967 on, excluding 1972.

The samples from the landsmen's hunt and large vessel hunt were first summed for each year, then reduced to their respective percentage compositions. These compositions were then weighted in accordance with the numbers of animals killed in the landsmen's and large vessel hunt (summed across ages) and subsequently divided by the sum of weighting factors. In this way, then, the age composition data gave the best possible representation of the catch distribution as the hunt has shifted from large vessels to landsmen (Fig. 2). Using this catch distribution the total catch was broken down into catch at age (Table 3).

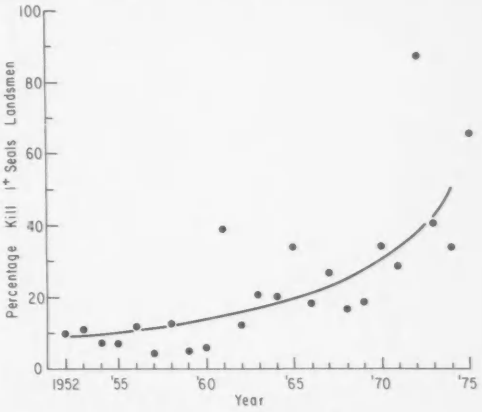

FIG. 2. Percentage of landsmen's kill in the total hunt of 1 yr and older harp seals from 1952 to 1975.

Biological Basis of the Model

CALCULATION OF NATURAL MORTALITY

The instantaneous rate of natural mortality is possibly the most elusive vital rate in population dynamics to estimate. Furthermore, for the harp seal population it is the most important due to the rather low exploitation rate experienced by 1+ animals.

The only representative sample of the population age distribution comes from males of age 2 and older in the molting patches (Benjaminsen and Øritsland 1975). Other calculations have been made using combined samples; however, these estimates are incorrect. Furthermore, it is assumed that there is no difference between natural mortality rates of male and female harp seals. This is a valid assumption as male and female harp seals seem to have similar growth rates and achieve equivalent maximum weights (Sergeant 1973a). The metabolic rate and body size of seals is well correlated (Lavigne et al. 1976), and since the mortality and metabolic rates of animals are related (Simms et al. 1959) it is unlikely that male or female harp seals experience divergent natural mortalities.

Male age samples of molting seals were taken from Benjaminsen and Øritsland (1975) for 1969–71 and 1973–74. In 1968, 1970, and 1973 there were also combined (male and female) samples that were corrected (Fig. 1) for the fraction of males. These corrected samples were added to the appropriate sexed male sample to produce a total male sample. The age frequencies were then reduced to percentage age compositions so the total instantaneous mortality rates (Z) could be calculated. Total instantaneous mortality rates, weighted for varying cohort abundance, were calculated by using the equation:

$$(1)\quad Z_{(t,t+1)} = \log_e \left[\sum_{i=2}^{i=24} P_t \Big/ \sum_{i=3}^{i=25} P_{t+1} \right]$$

where P is the percentage in year (t) for age (i). One-year-old animals were not included because of their erratic occurrence in the sample. Since there was not a representative male sample in 1972, the total mortality was calculated from 1971 to 1973 and the resulting value divided by two.

The weighted annual instantaneous mortality rates were as follows:

Year	Total mortality (Z)	
1968–69	0.0667	$z = 0.160$
1969–70	0.2247	
1970–71	0.1882	
1971–73	0.0892 (avg)	$z = 0.137$
1973–74	0.1836	

The following two simultaneous equations could then be constructed and solved:

$$\bar{F}_{68-71} + M = 0.160$$

$$\bar{F}_{71-74} + M = 0.137$$

where $\bar{F}$ is the average instantaneous rate of hunting mortality. Following the implementation of the quota regulations in 1971, hunting effort exerted on 1+ seals was essentially halved such that $\bar{F}_{68-71} = 2\bar{F}_{71-74}$. Hunting effort was calculated by multiplying the number of men by the

TABLE 1. Catch at age of the northwest Atlantic harp seal (*Pagophilus groenlandicus*) from different landsmen and large vessel fisheries. Individual samples are shown from 1961 on. Annual percentage compositions have been weighted in relation to the ratio of landsmen to larger vessel catch.

Age	Large vessel A	Landsmen A	% 1952	Large vessel A	Landsmen A	% 1953	Large vessel A	Landsmen A	% 1954	Large vessel A	Landsmen A	% 1955
1	10	27	4.29	419	15	27.61	233	15	35.76	30.71%	48	29.28
2	24	95	10.57	124	52	8.71	91	26	14.28	13.99	77	14.07
3	15	98	6.96	103	98	7.86	26	23	4.31	7.70	98	8.48
4	11	114	5.49	61	108	5.22	36	57	6.52	6.02	41	6.16
5	13	115	6.30	62	111	5.32	19	45	3.63	4.90	58	5.34
6	25	101	11.03	48	100	4.28	24	33	4.26	4.20	35	4.38
7	17	96	7.75	43	86	3.80	21	40	3.92	3.64	30	3.79
8	17	81	7.61	48	51	3.72	20	23	3.39	3.28	39	3.57
9	12	60	5.40	47	50	3.65	13	16	2.27	2.94	13	2.91
10	14	54	6.15	39	41	3.02	21	10	3.31	2.72	14	2.72
11	12	60	5.40	51	28	3.66	8	8	1.37	2.46	10	2.43
12	3	42	1.60	28	34	2.22	18	7	2.87	2.27	13	2.29
13	3	21	1.41	22	22	1.69	18	5	2.84	2.10	2	1.99
14	5	12	2.13	17	19	1.33	9	4	1.45	1.96	3	1.87
15	9	24	3.86	33	34	2.55	12	4	1.90	1.82	5	1.77
16	3	12	1.32	37	10	2.54	16	0	2.44	1.74	4	1.67
17	5	15	2.16	26	14	1.86	7	2	1.11	1.54	3	1.48
18	4	8	1.69	16	11	1.17	2	5	0.40	1.34	4	1.31
19	2	8	0.88	12	6	0.85	8	2	1.26	1.26	2	1.21
20	11	12	4.56	50	39	3.72	4	8	0.76	1.01	2	0.97
21	3	6	1.26	32	7	2.22	2	3	0.36	0.76	4	0.76
22	0	6	0.05	18	3	1.21	2	2	0.34	0.67	3	0.67
23	1	4	0.44	12	7	0.87	5	1	0.78	0.50		0.47
24	3	2	1.23	9	3	0.62	1	0	0.15	0.42		0.39
25	1	4	0.44	5	1	0.33	2	1	0.32	0.06		0.05

TABLE 1 (*Continued*)

Age	Large vessel A	Landsmen A	% 1956	Large vessel A	Landsmen A	% 1957	Large vessel A	Landsmen A	% 1958	Large vessel A	Landsmen A	% 1959	Large vessel A	Landsmen A	% 1960
1		11	27.42		11	29.78	40	26	15.43		9	29.37		34	19.49
2		59	13.42		20	13.46	15	25	7.14		23	13.74		107	9.12
3		62	7.88		23	7.67	19	90	4.01		25	7.79		67	5.17
4		55	6.27		26	6.11	22	142	3.19		18	6.06		202	4.02
5		37	4.97		17	4.91	18	110	2.57		23	5.09		47	3.36
6	AVG	35	4.32	AVG	15	4.21	11	115	2.21	AVG	26	4.48	AVG	62	2.97
7		42	3.94		21	3.77	11	82	1.97		25	3.93		41	2.60
8		54	3.82		17	3.36	9	81	1.76		22	3.52		19	2.34
9		45	3.37		16	3.03	9	58	1.59		21	3.19		14	2.11
10		33	2.97		21	2.88	17	69	1.51		17	2.90		18	1.92
11		23	2.58		21	2.64	13	63	1.38		10	2.53		13	1.67
12		30	2.52		18	2.42	14	45	1.26		7	2.29		12	1.52
13		19	2.19		12	2.18	8	40	1.13		5	2.09		6	1.39
14		20	2.07		16	2.09	6	31	1.10		9	2.03		9	1.35
15		11	1.80		14	1.93	16	27	1.01		7	1.86		4	1.23
16		20	1.88		9	1.78	14	14	0.90		4	1.72		5	1.15
17		15	1.62		8	1.58	6	18	0.80		4	1.54		3	1.02
18		25	1.62		8	1.39	1	13	0.72		2	1.32		3	0.87
19	AVG	15	1.37	AVG	6	1.29	3	5	0.67	AVG	3	1.25	AVG	0	0.83
20		16	1.17		11	1.11	9	15	0.58		2	0.99		4	0.66
21		10	0.84		6	0.85	7	3	0.42		0	0.72		0	0.48
22		8	0.73		5	0.71	6	3	0.37		0	0.64		1	0.42
23		9	0.60		0	0.48	2		0.25		1	0.50		0	0.33
24		7	0.49		2	0.43	4		0.22		0	0.40		0	0.27
25		3	0.10		3	0.09	2		0.05		1	0.07		0	0.05

TABLE 1 (*Continued*)

Age	Large vessel A	Landsmen A	% 1961	Large vessel A	Landsmen A	Landsmen B	Total landsmen	% 1962	Large vessel A	Landsmen A	Landsmen B	Total landsmen	% 1963	Large vessel A	Landsmen A	Landsmen B	Total landsmen	% 1964
1	122	16	26.35	201	20	6	26	23.55	111	18	26	44	7.93	3	10	43	53	3.13
2	34	65	10.39	245	50	15	65	29.17	121	52	83	135	10.28	6	31	42	73	5.53
3	25	100	10.27	61	74	16	90	8.25	106	86	54	140	9.42	8	74	50	124	7.97
4	30	126	12.62	56	95	30	125	8.15	55	90	33	123	5.83	11	64	32	96	9.30
5	11	39	4.27	39	95	21	116	6.07	46	80	26	106	4.93	7	65	32	97	6.72
6	13	52	5.34	17	33	7	40	2.60	61	56	21	77	5.35	12	40	42	82	9.65
7	15	43	5.30	15	46	14	60	2.54	67	32	8	40	5.04	6	27	29	56	5.15
8	9	27	3.24	16	42	16	58	2.63	66	36	10	46	5.09	5	11	35	46	4.28
9	8	28	3.08	17	29	13	42	2.53	63	22	12	34	4.67	5	10	23	33	4.00
10	17	24	4.76	6	18	16	34	1.15	72	25	15	40	5.36	8	6	27	33	5.95
11	10	15	2.84	8	14	10	24	1.24	70	24	14	38	5.20	4	11	18	29	3.25
12	3	20	1.63	13	17	3	20	1.77	51	20	10	30	3.83	4	5	21	26	3.19
13	4	16	1.64	6	11	11	22	0.99	57	11	9	20	4.03	3	6	20	26	2.53
14	6	7	1.61	9	13	8	21	1.32	56	17	14	31	4.17	3	3	21	24	2.48
15	1	12	0.81	12	21	23	44	1.98	42	22	11	33	3.31	5	4	7	11	3.50
16	5	5	1.29	4	7	10	17	0.69	54	15	9	24	3.91	4	2	11	13	2.90
17	4	3	0.98	12	9	4	13	1.56	36	13	11	24	2.76	5	4	12	16	3.62
18	2	2	0.52	5	11	4	15	0.78	24	9	4	13	1.78	8	1	6	7	5.37
19	3	0	0.63	4	1	6	7	0.56	18	4	12	16	1.45	4	0	14	14	2.92
20	2	7	0.77	9	4	12	16	1.26	18	10	10	20	1.53	0	2	6	8	0.18
21	0	0	0.21	1	1	2	3	0.16	17	5	6	11	1.30	4	0	6	6	2.74
22	2	0	0.42	4	6	5	11	0.61	12	5	8	13	1.01	2	2	3	5	1.42
23	1	2	0.31	0	1	3	4	0.17	9	4	10	14	0.84	2	0	5	5	1.42
24	0	1	0.26	1	1	2	3	0.16	8	2	6	8	0.66	3	1	2	3	2.02
25	1	4	0.41	1	2	3	5	0.18	4	1	2	3	0.31	1	0	6	6	0.79

TABLE 1 (*Continued*)

Age	Large vessel A	Landsmen A	% 1961	Large vessel A	Landsmen A	Landsmen B	Total landsmen	% 1962	Large vessel A	Landsmen A	Landsmen B	Total landsmen	% 1963	Large vessel A	Landsmen A	Landsmen B	Total landsmen	% 1964
1	32	4	4	8	13.21	120	10	1	11	15.30	176	55	231	17	12	6	35	18.53
2	13	17	10	27	6.58	100	29	2	31	13.75	61	31	92	14	42	11	67	8.68
3	13	45	24	69	8.72	39	42	3	45	6.86	18	5	23	1	46	17	64	3.34
4	15	72	34	106	11.42	40	44	5	49	7.17	18	6	24	9	37	24	70	3.56
5	23	71	24	95	14.06	45	42	7	49	7.79	29	19	48	11	58	30	99	6.11
6	22	66	18	84	13.09	45	50	5	55	8.06	46	22	68	21	72	25	118	8.11
7	7	39	15	54	5.56	44	33	4	37	7.15	40	19	59	26	64	27	117	7.39
8	2	32	16	48	3.25	31	19	0	19	4.69	30	13	43	21	43	14	78	5.21
9	2	18	4	22	1.92	15	14	4	18	2.67	23	5	28	26	31	10	67	3.79
10	5	9	5	14	2.72	17	8	2	10	2.55	16	8	24	16	27	9	52	3.12
11	1	10	5	15	1.17	23	10	1	11	3.34	34	13	36	21	14	11	46	3.89
12	7	12	6	18	3.72	17	5	0	5	2.32	18	6	24	14	15	5	34	2.67
13	1	16	7	23	1.18	15	7	0	7	2.17	14	5	19	16	10	6	32	2.24
14	5	8	7	15	2.76	17	7	0	7	2.42	19	10	29	15	16	7	38	3.15
15	4	8	10	18	2.52	14	7	0	7	2.05	20	10	30	13	12	7	32	3.08
16	2	6	6	12	1.41	14	7	1	8	2.09	14	6	20	17	4	6	27	2.19
17	1	5	5	10	0.91	10	3	2	5	1.46	18	8	26	12	9	3	24	3.34
18	3	2	4	6	1.51	17	1	0	1	2.14	20	9	29	9	7	4	20	2.71
19	3	6	4	10	1.71	10	1	2	3	1.37	21	9	30	8	4	6	18	2.74
20	1	3	1	4	0.60	11	2	0	2	1.45	15	4	19	11	5	4	20	1.95
21	2	3	2	5	1.06	8	1	0	1	1.03	8	4	12	3	3	4	10	1.16
22	1	1	1	2	0.50	3	1	1	2	0.46	8	1	9	2	4	0	6	0.84
23	0	2	0	2	0.10	7	1	0	1	0.91	8	3	11	3	0	1	4	0.94
24	0	1	2	3	0.15	4	0	0	0	0.49	4	2	6	5	2	2	9	0.68
25	0	1	2	3	0.15	2	0	2	2	0.34	4	2	6	1	3	1	5	0.58

TABLE 1 (*Continued*)

Age	Large vessel		Total large vessel	Landsmen		Total landsmen	% 1968	Large vessel		Total large vessel	Landsmen				Total landsmen	% 1969
	A	B		A	B			A	B		A	B	C	D		
1	84	142	226	7	11	18	15.04	62	396	458	87	37	9	5	138	35.77
2	77	78	155	8	48	56	11.37	2	56	58	13	14	20	4	51	5.10
3	48	43	91	8	68	76	7.71	6	40	46	13	21	49	29	112	5.26
4	20	27	47	8	56	64	4.58	1	32	33	13	10	69	18	110	4.28
5	17	32	49	5	39	44	4.23	2	43	45	11	11	71	11	104	5.05
6	23	20	43	9	54	63	4.30	4	30	34	10	2	49	6	67	3.62
7	27	48	75	12	41	53	6.13	1	38	39	5	5	60	11	81	4.22
8	39	38	77	15	39	54	6.28	6	45	51	7	4	59	10	80	5.08
9	23	31	54	16	17	33	4.29	2	39	41	1	2	43	11	57	3.96
10	26	30	56	15	18	33	4.42	0	29	29	6	11	40	2	59	3.12
11	19	23	42	10	14	24	3.30	3	24	27	4	6	38	3	51	2.84
12	18	12	30	13	14	27	2.59	1	18	19	4	2	22	6	34	1.97
13	16	16	32	9	7	16	2.46	2	21	23	5	5	20	1	31	2.21
14	24	18	42	7	9	16	3.10	2	24	26	3	2	16	1	22	2.27
15	20	15	35	9	10	19	2.72	2	24	26	3	1	24	0	28	2.37
16	20	14	34	11	6	17	2.61	2	16	18	2	1	18	1	22	1.69
17	11	17	28	10	9	19	2.27	0	24	24	6	5	11	0	22	2.13
18	17	27	44	7	4	11	3.11	0	21	21	2	0	11	1	14	1.77
19	16	22	38	5	5	10	2.70	0	22	22	3	2	5	0	10	1.78
20	11	16	27	3	2	5	1.87	0	20	20	2	0	4	1	7	1.58
21	6	11	17	4	1	5	1.22	1	13	14	2	0	5	1	8	1.16
22	5	19	24	4	3	7	1.72	2	10	12	1	1	2	0	4	0.94
23	4	10	14	2	0	2	0.95	2	9	11	2	0	0	0	2	0.84
24	2	8	10	1	0	1	0.67	1	5	6	0	0	1	0	1	0.45
25	1	4	5	0	1	1	0.35	0	7	7	0	1	0	0	1	0.53

TABLE 1 (*Continued*)

Age	Large vessel A	Large vessel B	Total large vessel	Landsmen A	Landsmen B	Landsmen C	Landsmen D	Total landsmen	% 1970	Large vessel	Landsmen A	Landsmen B	Landsmen C	Landsmen D	Total landsmen	% 1971	Large vessel	Landsmen A	Landsmen B	Landsmen C	Total landsmen	% 1972
1	105	134	239	41	31	5	21	98	18.17	239	3	4	17	39	63	31.59	12	11	1	0	12	6.21
2	98	112	210	41	69	12	60	182	17.46	66	18	15	29	27	89	10.72	9	19	6	3	28	8.10
3	11	34	45	15	89	32	67	203	6.29	53	35	51	45	33	164	11.19	9	17	2	1	20	14.27
4	17	29	46	25	45	55	63	188	6.13	19	34	30	17	14	95	5.02	24	26	3	3	32	9.88
5	18	15	33	23	40	77	68	208	5.53	18	45	32	31	5	113	5.37	9	10	1	6	17	10.07
6	12	18	30	19	16	38	44	117	3.91	11	30	9	9	21	69	3.30	10	15	0	3	18	6.54
7	15	26	41	14	8	35	24	81	4.12	10	16	9	6	18	49	2.61	13	5	0	4	9	5.15
8	8	15	23	43	12	64	22	141	3.79	8	23	4	6	15	48	2.34	9	8	0	3	11	4.72
9	13	22	35	49	8	66	25	148	4.74	17	21	7	3	13	44	3.35	6	5	1	0	6	4.14
10	18	13	31	49	8	82	24	153	4.54	16	30	3	4	31	58	3.61	6	6	0	1	7	5.29
11	13	7	20	24	4	61	13	102	2.97	10	9	2	10	20	41	2.39	4	13	0	2	15	3.72
12	20	6	26	28	4	42	8	82	3.09	12	6	6	2	26	40	2.61	5	7	0	6	13	3.72
13	12	11	23	26	1	37	8	72	2.72	8	8	6	4	22	40	2.11	2	5	0	2	7	3.46
14	6	10	16	19	0	30	5	54	1.95	4	9	3	0	13	25	1.20	2	15	0	0	15	2.23
15	11	13	24	29	2	32	10	73	2.81	6	4	3	0	18	25	1.45	6	6	0	2	8	2.57
16	13	4	17	30	1	27	2	60	2.12	6	3	5	0	11	19	1.28	4	3	1	0	4	1.91
17	7	8	15	20	0	30	9	59	1.96	6	5	3	1	8	17	1.22	3	8	0	0	8	1.66
18	7	10	17	12	1	21	6	40	1.81	9	4	1	0	10	15	1.54	2	7	0	3	10	1.41
19	7	7	14	18	1	17	6	42	1.63	6	3	2	0	7	12	1.08	0	5	0	0	5	0.99
20	6	6	12	22	3	16	6	47	1.56	8	2	0	1	11	14	1.39	5	13	0	1	14	1.58
21	4	4	8	10	1	10	1	22	0.90	5	0	0	2	7	9	0.87	1	7	1	1	9	0.83
22	5	2	7	5	0	9	1	15	0.72	9	0	0	0	4	4	1.23	3	3	0	2	5	0.59
23	3	0	3	7	0	4	3	14	0.43	7	0	0	0	4	4	0.99	1	2	0	2	2	0.41
24	3	1	4	5	0	5	1	11	0.45	4	1	0	0	1	2	0.56	2	3	0	0	3	0.34
25	0	1	1	3	0	6	0	9	0.21	7	1	0	0	2	3	0.96	0	0	0	0	0	0.25

TABLE 1 (*Continued*)

Age	Large vessel		Total large vessel	Landsmen	%	Large vessel	Landsmen				Total	%	Large vessel	Landsmen					Total	%
	A	B		A	1973	A	A	B	C	D	landsmen	1974	A	A	B	C	D	E	landsmen	1975
1	171	4	175	6	6.52	360	0	8	46	106	160	26.66	464	20	0	157	146	55	378	28.80
2	232	5	237	14	9.61	227	0	18	33	22	73	15.62	223	55	1	123	30	47	256	17.10
3	188	0	188	16	8.40	86	2	7	11	7	27	5.89	102	56	12	61	13	20	162	9.79
4	173	5	178	9	6.98	65	5	10	10	5	30	4.86	67	19	26	40	1	10	96	5.98
5	293	6	299	11	11.26	67	17	12	5	6	40	5.40	57	8	62	29	4	4	107	6.20
6	81	0	81	11	4.16	88	61	19	7	4	91	8.73	57	4	57	25	2	5	93	5.58
7	67	1	68	16	4.34	21	20	13	3	1	37	2.73	28	5	71	22	1	9	108	5.48
8	79	6	85	15	4.61	21	30	18	3	0	51	3.33	23	4	50	11	0	2	67	3.55
9	42	0	42	21	4.16	36	19	17	1	0	37	3.56	29	3	21	7	0	2	33	2.21
10	37	4	41	17	3.47	21	15	20	0	0	35	2.65	17	0	19	18	0	10	47	2.07
11	45	3	48	24	4.65	16	8	18	0	1	27	2.03	28	0	14	14	0	1	29	2.01
12	30	0	30	27	4.54	24	11	14	2	0	27	2.47	17	2	14	11	0	4	31	1.81
13	36	0	36	22	4.09	23	6	17	1	0	24	2.29	20	0	10	20	1	1	32	1.93
14	24	0	24	21	3.56	19	2	17	1	0	20	1.90	15	0	9	18	0	0	27	1.58
15	36	1	37	18	3.56	30	2	16	0	0	18	1.86	15	0	5	10	0	0	15	1.05
16	32	1	33	15	3.04	16	2	21	0	1	24	1.90	13	0	7	7	0	2	16	1.04
17	25	1	26	11	2.28	16	4	13	1	0	18	1.65	13	0	1	7	0	1	9	0.74
18	23	1	24	10	2.08	14	1	10	0	0	11	1.24	10	0	7	9	0	0	16	0.97
19	29	1	30	6	1.76	12	2	7	0	0	9	1.04	8	0	2	4	0	0	6	0.47
20	33	0	33	6	1.89	10	1	6	0	0	7	0.85	6	0	0	4	0	1	5	0.38
21	18	0	18	3	0.99	8	0	8	0	0	8	0.78	5	0	0	3	0	0	3	0.26
22	18	0	18	13	0.23	9	0	7	0	0	7	0.79	7	0	1	2	0	0	3	0.32
23	20	0	20	0	0.67	7	0	4	0	0	4	0.56	5	0	0	0	0	1	1	0.18
24	15	0	15	0	0.50	11	0	0	0	0	0	0.61	6	0	1	2	0	0	3	0.29
25	17	0	17	0	0.56	9	1	1	0	0	2	0.58	5	0	0	2	0	0	2	0.22

TABLE 1 (*Concluded*)

Age	Large vessel A	Landsmen A	B	C	D	E	Total landsmen	% 1976
1	292	0	7	88	75	113	283	33.20
2	112	0	18	57	34	58	167	18.96
3	60	1	26	45	20	25	117	12.08
4	35	13	9	37	11	17	87	8.73
5	24	16	4	22	2	2	46	4.76
6	13	15	3	20	1	0	39	3.84
7	18	19	1	10	1	0	31	3.26
8	13	13	0	16	2	0	31	3.12
9	11	9	1	3	0	0	13	1.46
10	6	14	1	9	0	0	24	2.30
11	6	8	0	6	2	0	16	1.59
12	5	4	0	5	2	0	11	1.12
13	8	5	0	3	0	0	8	0.93
14	5	4	0	4	1	0	9	0.94
15	5	3	0	13	0	0	16	1.57
16	5	1	0	4	0	0	5	0.58
17	5	1	0	5	0	0	6	0.67
18	3	0	0	4	0	0	4	0.44
19	2	0	0	4	0	0	4	0.41
20	1	0	0	5	0	0	5	0.47
21	1	0	0	1	0	0	1	0.12
22	2	0	0	1	0	0	1	0.14
23	1	0	0	1	0	0	1	0.16
24	0	0	0	1	0	0	1	0.09
25	0	0	0	1	0	0	1	0.09

TABLE 2. Total catch of 1+ northwest Atlantic harp seals by landsmen and large vessels from 1952 to 1975.

	Landsmen	Large vessel	% Landsmen	% Large vessel
1952	10667	98378	9.8	90.2
53	8100	66811	10.8	89.2
54	5443	83939	6.1	93.9
1955	5401	75671	6.7	93.3
56	5428	42585	11.3	88.7
57	3605	76437	4.5	95.5
58	19563	137227	12.5	87.5
59	3998	77304	4.9	95.1
1960	6648	114534	5.5	94.5
61	5877	13170	30.9	69.1
62	13388	99513	11.9	88.1
63	14529	57094	20.3	79.7
64	14933	60348	19.8	80.2
1965	17738	33757	34.4	65.6
66	12647	59364	17.6	82.4
67	15245	41361	26.9	73.1
68	5910	30328	16.3	83.7
69	10532	44940	19.0	81.0
1970	13839	26225	34.5	65.5
71	6044	14343	29.6	70.4
72	11427	1646	87.4	12.6
73	10416	15081	40.9	59.1
74	10982	21828	33.5	66.5
1975	22733	10992	67.4	32.6

length of time they hunted 1+ seals and the mean horsepower of the vessels. This value was then divided by the mean tonnage of the vessels, the number of days was calculated according to the closing dates of the hunt, and the other values were taken from ICNAF statistical yearbooks. Ice condition was not considered in the calculation because of the lack of data; however, its inclusion would presumably greatly improve the calculation of effective effort. The hunting effort, which varies little from year to year, was 120,000 men $\times$ day $\times$ hp $\times$ ton^{-1} between 1961 and 1970, and 56,000 between 1972 and 1975. In both cases the standard deviation was only (8900 men $\times$ day $\times$ hp) $\times$ ton^{-1}. Thus the change in effort is 2.07 and the assumption of a halving of effort between the two periods seems quite valid. The two equations then give the following values:

$$M = 0.114 \text{ and } \bar{F}_{68-71} = 0.046 \text{ and } \bar{F}_{71-74} = 0.023.$$

By subtracting the appropriate F value from the Z values 0.0677 SD (standard deviation) and 0.0302 SE (standard error) were calculated.

Using a method devised by Ricker (1971), Benjaminsen and Øritsland (1975) calculated natural mortality to be 0.102 with 0.011 SD. For this reason, in addition to our limited sample size, it is assumed that the standard error more closely represents the real deviation in natural mortality. Furthermore, we assume the deviation to be normally distributed since, if the level of natural mortality is biologically determined, resulting from a population control mechanism, the true distribution of values would tend to have a central tendency. Other calculations of natural mortality are somewhat lower, near 8%/yr (Ricker 1971; Ulltang 1971).

Lavigne et al. (1976) present an age-specific natural mortality schedule which declines from 0.2 for O-group seals to 0.095 for 5–6 yr olds. Following this, mortality rises to 0.109 for adults and remains constant. This schedule, although assumed, makes good biological sense since mortality and growth are usually coupled (Simms et al. 1959; Bourlière 1959). For harp seals the growth rate begins to slow down at the onset of maturity. According to Lavigne et al. (1976), the instantaneous growth rate of mature seals is 0.12, not far from our estimated mortality of 0.114. However, at some point the mortality rate must exceed growth rate or the biomass of the cohort of seals would continue to increase forever. Senescent death in harp seals may begin at approximately age 18, if one speculates as to the reason for inflection in the survivorship curve at this time. Thus the critical age for a cohort of seals probably is near 18 yr. In our analysis we could find no evidence of an age-dependent natural mortality rate, which is not surprising considering the crudity of catch data and the delicate changes in the vital rate as suggested by Lavigne et al. (1976). However, the analysis was on 2+ seals and a different mortality rate may be experienced by the younger animals. There is evidence, although it is not strong enough to present in this paper as fact, that mortality in the 1st yr is density dependent and it indeed is less than that of older seals when pup catches are high.

SEQUENTIAL POPULATION ANALYSIS

Sequential population methods (Murphy 1964; Jones 1964; Gulland 1965; Pope 1972; Doubleday 1975) were developed to estimate fish population sizes and fishing mortalities from catch-at-age data when good effort data are not available. Although there are no examples of this method being used to assess mammalian populations, no assumptions are violated by its use. For this reason it may be instructional to outline the method.

The sequential population analysis developed by Pope (1972), called cohort analysis, was utilized in this study since it assumes that natural and hunting mortality occur somewhat season-

ally, which is true to a great extent in the seal fishery. The method is based on the formula:

$$(2) \quad N_i = C_i \exp(M/2) + N_{i+1} \exp(M)$$

where N_i is the population of a year-class at the i^{th} birthday, C_i is the catch of a cohort at age i, and M is the instantaneous rate of natural mortality. This formula is applied sequentially, the cohort size within an age-group in each year depending on the cohort size within the age-group the year after. However, some starting values are required. Thus, by expanding equation (2):

$$(3) \quad N_i = (C_i \exp(M/2) + C_{i+1} \exp(3M/2) + C_{i+2} \exp(5M/2) + \ldots + N_t \exp((t - i)M)$$

and assuming that hunting does not completely extirpate a particular cohort, the last term for the final year's population is:

$$(4) \quad N_i = \frac{C_i(F_{i+1} + M)}{F_i(1 - \exp(-F_{i+1} - M))}.$$

Equation 4, then, is used to calculate the population size in the initial year. Thus, one of the primary problems is to estimate starting hunting mortality values.

The average hunting mortality calculated for 1972–74 was 0.023 and it was assumed that this value also applied in 1975. The analysis was not started using the 1976 data since all samples are not yet completely analyzed. When possible, considerable care should be given in estimating the initial hunting mortality since hunting mortalities are low for harp seals and the analysis is therefore more sensitive to initial F for a longer period. However, when the data series is long, poor starting values of F are considerably improved as the analysis continues. After running the analysis and averaging hunting mortalities for ages 10–20 it was determined that on average a hunting mortality of 0.02 was adequate for animals of age 25. The age-specific hunting mortalities calculated by the formula:

$$(5) \quad F = \log_e(N_i/N_{i+1}) - M$$

are presented in Table 4.

The resultant population estimates (Table 5) indicate that there was a dramatic decline, such that in 1968 the herd was only 45% as large as its size in 1952. Pup production estimated by cohort analysis is somewhat erratic (Fig. 3), indeed more than would be expected for a mammalian population. This inconsistency can perhaps be attributed to a natural mortality rate among pups which responds in some way to the exploitation rate. Furthermore, interspecific competition may be a factor in determining resultant natural mortality rates.

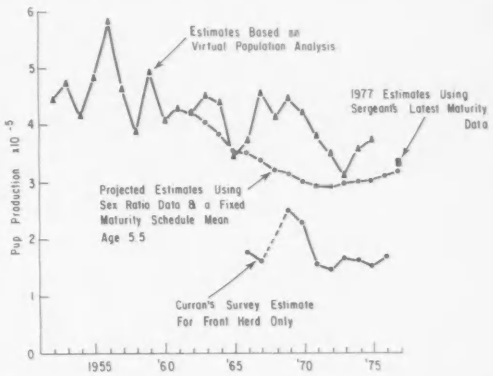

FIG. 3. Comparison of three different methods of estimated pup production.

DENSITY-DEPENDENT PREGNANCY AND WHELPING AGE

It has been proposed by Sergeant (1966, 1973b) that the mean age of whelping for harp seals is a density-dependent function relying on population size. This phenomenon is well noted in some other marine mammals (Gambell 1973). Certainly, some sort of mechanism is necessary to equilibrate the population with the carrying capacity of its environment (McLaren 1967). Sergeant (1976) presented further evidence that the mean age of whelping has shifted to an extremely low level of 4.8 yr in 1976, a figure well below the 6.5 yr calculated in 1953. However, the reason for this most recent shift from 1968–76 is not clear since the population has stabilized and seems to be increasing slightly. Furthermore, it will not become lucid until some information on the growth rate of individuals within cohorts becomes available. Sergeant (personal communication) has suggested that the maturity schedule of seals is determined by their growth rate as juveniles since growth approaches an asymptote at about age 5 (Sergeant 1973a). Lavigne et al. (1976) also suggest an age of 5. In both examples the data are extremely variable. The harp seal population did reach its minimum level of 1.07 million 1+ seals between 1966 and 1973 (Table 5). Assuming that the growth rate of juvenile seals is stock dependent, this would suggest that Sergeant's hypothesis is possibly correct. Until more conclusive evidence concerning the reproductive biology of harp seals is presented, we assume that the maturity schedule of harp seals is dependent on the coincident popula-

TABLE 3. Catch-at-age data of the northwest Atlantic harp seal resulting from the weighting of samples and application to the total catch.

Age	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
0	198063	197975	184491	260020	346846	171909	149350	243255	164158	174762	211285	285994
1	4679	20685	35353	26005	14664	25488	44871	25180	37848	6586	27588	6780
2	11529	6527	14119	12499	7175	11796	20701	11778	18220	2597	34154	8785
3	7589	5888	4257	7526	4215	6631	12830	6675	10108	2566	9762	8044
4	5983	3913	6444	5467	3355	5280	11387	5194	9486	3155	9549	4980
5	6875	3988	3590	4738	2660	4248	9163	4360	6478	1067	7108	4215
6	12029	3207	4207	3889	2310	3647	8247	3838	5783	1335	2932	4572
7	8451	2843	3879	3367	2108	3256	6812	3365	4877	1326	2978	4308
8	8302	2790	3351	3171	2045	2908	6268	3021	4200	811	3081	4349
9	5889	2732	2246	2588	1804	2618	5347	2731	3737	771	2963	3993
10	6711	2263	3271	2414	1588	2493	5231	2485	3506	1192	1350	4582
11	5889	2741	1350	2159	1378	2285	4754	2168	3145	712	1462	4440
12	1740	1664	2841	2031	1369	2088	4129	1961	2896	409	2075	3272
13	1532	1267	2806	1763	1169	1877	3792	1792	2627	411	1160	3440
14	2325	996	1430	1659	1112	1809	3419	1741	2488	403	1550	3562
15	4208	1909	1882	1567	964	1670	3141	1595	2264	204	2319	2828
16	1443	1901	2415	1485	1006	1541	2774	1479	2172	325	810	2240
17	2355	1395	1092	1311	867	1367	2566	1319	1912	248	1829	2355
18	1844	879	391	1161	865	1205	2188	1128	1673	130	914	1522
19	962	640	1243	1068	734	1112	1916	1075	1538	157	652	1242
20	4971	2786	746	859	624	964	1741	854	1273	193	1470	1306
21	1383	1630	356	674	450	696	1150	617	923	53	183	1107
22	60	909	338	592	392	615	1028	548	831	105	715	865
23	481	649	773	418	321	417	842	427	616	78	199	717
24	1344	468	151	348	263	371	702	343	513	65	183	566
25	481	254	320	47	54	83	157	62	69	103	215	267

TABLE 3 (*Concluded*)

Age	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
0	270952	187284	225250	279858	159971	236532	220520	213349	119658	102744	118036	140629
1	2502	7413	11558	10877	5980	20985	7844	7315	1990	1949	9604	9629
2	4418	3693	10383	5100	4521	2993	7535	2483	1289	2874	5629	5719
3	6364	4898	5183	1959	3069	3088	2714	2591	2272	2511	2123	3275
4	7429	6408	5414	2090	1823	2512	2644	1163	1573	2087	1752	1999
5	5364	7889	5880	3587	1682	2966	2387	1250	1604	3367	1945	2072
6	7702	7349	6086	4760	1711	2125	1687	764	1041	1243	3144	1867
7	4117	3121	5373	4341	2437	2479	1776	606	820	1299	985	1832
8	3419	1826	3543	3059	2498	2983	1637	542	752	1380	1200	1186
9	3189	1081	2018	2227	1705	2325	2045	776	659	1245	1283	740
10	4751	1524	1928	1830	1757	1831	1958	837	842	1038	954	693
11	2597	655	2522	2282	1310	1666	1286	554	592	1392	732	672
12	2544	2088	1756	1570	1031	1153	1332	606	593	1360	891	605
13	2023	660	1639	1316	976	1295	1175	490	552	1224	825	646
14	1988	1553	1825	1852	1233	1333	844	277	355	1064	685	529
15	2799	1415	1548	1810	1082	1393	1211	335	410	1067	674	353
16	2314	794	1580	1289	1037	991	914	297	304	909	686	350
17	2887	512	1104	1964	903	1248	847	284	264	682	594	247
18	4290	846	1619	1592	1237	1039	780	357	224	623	447	323
19	2331	961	1035	1608	1073	1042	703	251	158	526	377	159
20	142	340	1094	1143	742	927	676	322	252	566	306	127
21	2189	593	780	684	485	680	389	203	132	298	282	88
22	1130	282	349	491	684	554	312	286	94	690	287	106
23	1130	58	687	552	379	491	185	229	67	201	201	59
24	1616	87	373	400	267	267	195	129	54	151	219	97
25	628	87	256	342	139	310	91	222	40	171	210	74

TABLE 4. Hunting mortality levels of the northwest Atlantic harp seal calculated from cohort analysis assuming $M = 0.114$.

Age	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
0	0.644	0.585	0.634	0.844	0.989	0.499	0.524	0.733	0.557	0.570	0.759	1.101
1	0.024	0.112	0.174	0.151	0.088	0.150	0.210	0.140	0.209	0.034	0.146	0.042
2	0.062	0.039	0.095	0.078	0.052	0.087	0.159	0.072	0.130	0.018	0.218	0.058
3	0.032	0.037	0.029	0.062	0.032	0.057	0.116	0.065	0.074	0.022	0.075	0.067
4	0.032	0.019	0.047	0.044	0.033	0.046	0.119	0.058	0.112	0.027	0.096	0.046
5	0.060	0.024	0.020	0.041	0.025	0.048	0.095	0.056	0.087	0.015	0.071	0.051
6	0.066	0.033	0.030	0.025	0.023	0.039	0.112	0.048	0.089	0.021	0.047	0.055
7	0.084	0.019	0.047	0.027	0.016	0.038	0.086	0.056	0.072	0.024	0.053	0.082
8	0.055	0.033	0.025	0.045	0.019	0.024	0.086	0.046	0.084	0.014	0.066	0.092
9	0.066	0.022	0.031	0.022	0.030	0.028	0.051	0.045	0.067	0.018	0.060	0.103
10	0.049	0.030	0.029	0.038	0.016	0.048	0.065	0.028	0.068	0.025	0.036	0.112
11	0.063	0.023	0.021	0.022	0.025	0.025	0.110	0.032	0.041	0.016	0.035	0.145
12	0.035	0.021	0.028	0.036	0.016	0.044	0.053	0.055	0.049	0.006	0.052	0.091
13	0.014	0.030	0.041	0.020	0.024	0.025	0.096	0.027	0.089	0.008	0.019	0.103
14	0.038	0.010	0.039	0.028	0.014	0.042	0.053	0.054	0.043	0.016	0.033	0.068
15	0.093	0.036	0.022	0.050	0.019	0.024	0.087	0.029	0.083	0.004	0.109	0.070
16	0.058	0.051	0.054	0.019	0.038	0.034	0.047	0.050	0.046	0.014	0.018	0.132
17	0.133	0.066	0.034	0.034	0.013	0.060	0.067	0.026	0.076	0.006	0.088	0.059
18	0.140	0.061	0.022	0.042	0.026	0.020	0.117	0.035	0.038	0.006	0.024	0.090
19	0.045	0.061	0.105	0.070	0.031	0.039	0.037	0.071	0.056	0.004	0.032	0.037
20	0.383	0.159	0.085	0.090	0.049	0.048	0.071	0.019	0.102	0.008	0.043	0.075
21	0.186	0.188	0.025	0.094	0.057	0.064	0.067	0.030	0.024	0.005	0.008	0.038
22	0.014	0.163	0.050	0.049	0.066	0.094	0.115	0.038	0.047	0.003	0.077	0.044
23	0.023	0.188	0.185	0.073	0.031	0.085	0.163	0.059	0.050	0.005	0.005	0.094
24	0.090	0.026	0.056	0.108	0.055	0.041	0.183	0.085	0.085	0.006	0.013	0.016
25	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020

Age	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
0	1.038	0.861	1.019	1.039	0.528	0.826	0.809	0.900	0.448	0.426	0.428
1	0.020	0.058	0.099	0.101	0.045	0.108	0.049	0.048	0.008	0.011	0.058
2	0.032	0.034	0.098	0.053	0.051	0.026	0.047	0.018	0.010	0.026	0.035
3	0.050	0.041	0.056	0.022	0.038	0.041	0.028	0.019	0.019	0.022	0.022
4	0.074	0.059	0.053	0.027	0.024	0.036	0.041	0.014	0.013	0.020	0.018
5	0.059	0.096	0.065	0.042	0.025	0.045	0.040	0.023	0.021	0.032	0.021
6	0.113	0.097	0.091	0.063	0.023	0.036	0.030	0.015	0.022	0.019	0.035
7	0.058	0.056	0.087	0.079	0.038	0.038	0.035	0.012	0.018	0.031	0.017
8	0.079	0.030	0.076	0.060	0.055	0.054	0.030	0.012	0.017	0.035	0.033
9	0.083	0.030	0.039	0.057	0.040	0.060	0.044	0.016	0.017	0.033	0.037
10	0.156	0.048	0.062	0.041	0.054	0.050	0.061	0.021	0.020	0.030	0.029
11	0.078	0.027	0.094	0.089	0.034	0.060	0.041	0.020	0.017	0.038	0.025
12	0.106	0.076	0.084	0.071	0.048	0.035	0.057	0.023	0.025	0.045	0.028
13	0.069	0.033	0.072	0.077	0.053	0.072	0.041	0.025	0.024	0.059	0.032
14	0.073	0.063	0.109	0.099	0.087	0.087	0.056	0.012	0.012	0.052	0.039
15	0.064	0.062	0.075	0.137	0.071	0.123	0.097	0.026	0.019	0.072	0.039
16	0.069	0.021	0.984	0.076	0.099	0.078	0.101	0.029	0.027	0.048	0.055
17	0.228	0.018	0.034	0.129	0.064	0.151	0.081	0.038	0.029	0.071	0.037
18	0.132	0.088	0.066	0.057	0.102	0.089	0.122	0.041	0.035	0.081	0.056
19	0.175	0.036	0.135	0.079	0.046	0.107	0.073	0.048	0.021	0.097	0.059
20	0.005	0.032	0.048	0.197	0.044	0.046	0.086	0.040	0.057	0.088	0.069
21	0.158	0.023	0.087	0.035	0.109	0.047	0.023	0.031	0.019	0.080	0.053
22	0.045	0.025	0.016	0.066	0.041	0.160	0.025	0.019	0.017	0.117	0.095
23	0.067	0.003	0.072	0.028	0.061	0.034	0.067	0.021	0.005	0.040	0.042
24	0.284	0.006	0.020	0.050	0.016	0.051	0.016	0.056	0.006	0.013	0.052
25	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.020

tion size of 1+ animals. There is little evidence to suggest that the Front and Gulf herds experience a different maturity schedule, although this point may be argued by Sergeant (1973b). Thus the data utilized from these two areas were not weighted in relation to population size.

The ogives were plotted on "probit" paper and lines were fitted by eye, giving more weight to

points closer to the 50% maturity level. Values for each age were then interpolated from these lines, under the assumption that they represented the best fit of the data. The interpolated values were used to determine the following equation (Fig. 4):

$$(6)\quad \text{arc sine } {}_iE_t = 15.522A - 2.245 \times 10^{-5}N_t - 16.017$$

where ${}_iE_t$ is the fraction of the population whelping, assuming 100% pregnancy for a particular age i, N_t is the population number of 1+ seals in the year t, and A is the age in years.

The shift in maturity in response to population size is assumed to be linear since the best fit of the mean age of whelping over the data series was linear, although again the data are not conclusive. Capstick and Ronald (1976) fitted an exponential relationship to two data points, where there seems to be some confusion concerning the independent and dependent variables (see Fig. 4). In fact, the curve has doubtful biological meaning since, according to their hypothesis, the mean age of maturity approaches zero at population sizes less than 1 million, a result they previously speculate as being impossible. In addition, age of maturity reaches an asymptote at larger herd sizes, such that the population can increase ad infinitum. Surely the opposite effect is expected if it is indeed nonlinear, since the biological basis for a shifting maturity ogive would be to constrain the population within the environmental carrying capacity.

Density-dependent, age-specific maturity would be enough to limit the population, but this is only one of a multitude of factors. Others responding to population size could be natural mortality and fertility rate. Although we have no evidence for density-dependent mortality, there does seem to be some data supporting a varying fertility rate (Fig. 5). Fertility rates were determined from a number of sources (Fisher 1952; Sergeant 1966, 1969, 1970, 1976; Øritsland 1971). The response seems to be a linearly decreasing function of population size; however, the data are variable and the structure of the relationship is not clear. The data were plotted against the 2+ population size since the younger animals remain segregated from the herd and would not compete. A fluctuating fertility rate is a well-noted phenomenon and has been observed in at least three populations of whales (Gambell 1973). In addition, the unexploited population of Antarctic crabeater seals (*Lobodon carcinophagus*) which, like harp seals, also enjoys an unlimited ice substrate on which to whelp, has a low pregnancy rate of 0.76 (Øritsland 1970). Markgren (1969) found that the ovulation rate in moose (*Alces alces*) was related to a number of factors such as age, body size, nutrition, climate, and population density.

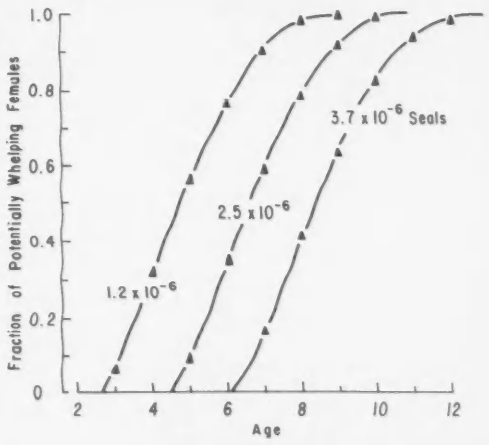

FIG. 4. A shifting maturity ogive in relation to population size. The ogive is constrained in the model so it cannot shift farther to the left than the 1.2×10^{-6} ogive level although the population may continue to decline.

EFFECTS OF CHANGING SEX RATIO ON POPULATION PROJECTION

The pup production estimates resulting from sequential population analysis are erratic (Fig. 3), possibly as a result of unaccountable fluctuations in natural mortality. In addition, the preponderance of males in the kill from molting seals would result in a sex ratio favoring females (Fig. 1). This could increase the estimates of pup production by 15,000 or 20,000 animals.

It is unlikely that there are serious errors in the catch distributions for seals 1–6 (Table 3), since only 8% of the variation of these data is unexplained when compared with the actual catch of bedlamers (see table 2, Øritsland and Benjaminsen 1975). This comparison is made by plotting the addition of the catch of 1–6 yr olds (Table 3) against the catch of bedlamers from 1952 to 1975 as calculated by Øritsland and Benjaminsen (1975). The functional regression (Ricker 1973) through these points has a slope not significantly different from unity and a position not significantly different from the origin. As previously noted, the best estimates from cohort analysis are between 1961 and 1975 since during this period the catch data are more consistent. Because the estimates of population improve as the analysis proceeds (Pope 1972), 1961 should then give the most reliable abundance level. With this in mind, a projection starting in 1961, subtracting the age-specific catch of the various

TABLE 5. Numbers at age of the northwest Atlantic harp seal estimated by cohort analysis from catch data (Table 3) assuming $M = 0.114$.

Age	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
0	441614	473555	416283	482960	584822	463624	387829	495879	407345	426122	420630	453722
1	211501	206945	235528	197163	185312	194184	251288	204969	212675	214060	215132	175732
2	205981	184294	165109	176757	151356	151495	149186	181829	159100	162175	184776	165893
3	259377	172898	158272	133983	145907	128271	124030	113559	151113	127367	142249	132606
4	205951	224263	148708	137199	112439	126205	108187	98548	95018	127365	111220	117787
5	125093	178110	196404	126599	117252	97155	107620	85775	83024	77614	110663	90217
6	201628	105121	155153	171852	108484	102107	82675	87370	72415	70886	68244	92025
7	112067	168542	90766	134462	149663	94613	87661	65978	74331	59444	61988	58122
8	164385	92010	147697	77322	116795	131547	81344	71782	55690	62201	51787	52496
9	98334	138832	79461	128619	65996	102279	114627	66659	61194	46345	54733	43297
10	151167	82177	121293	68778	112317	57182	88787	97226	56898	53117	40623	46037
11	102492	128541	71185	105135	59088	98715	48666	74280	84403	50227	46269	34971
12	53662	85887	112103	62241	91768	51420	85921	38932	64229	74773	44143	39903
13	123154	46237	75061	97341	53616	80607	43907	72764	32885	58040	66330	37427
14	66875	108438	40059	64324	85188	46735	70149	35595	63231	27271	51399	58088
15	50322	57474	95814	34392	55826	74959	39991	59362	30115	56353	23952	44397
16	27505	40925	49478	83713	29206	48901	65306	32716	51459	26229	50089	19181
17	20122	23178	34720	41866	73291	25109	42177	55649	27794	47867	23096	43927
18	14974	15729	19363	29948	36117	64575	21113	35209	48408	25001	42476	18880
19	23533	11619	13205	16908	25625	31409	56480	16771	30350	42072	22185	37036
20	16550	20089	9762	10608	14077	22171	26974	48585	13949	27586	37391	19179
21	8641	10071	15293	8006	8654	11971	18871	22424	42543	11600	24431	31974
22	4570	6404	7446	13309	6507	7296	10024	15752	19425	48332	10300	21626
23	22539	4021	4855	6325	11316	5435	5929	7973	13537	18218	43025	8515
24	16632	19656	2975	3602	5249	9794	4456	4495	6711	12943	18181	38202
25	25698	13570	17096	2511	2885	4435	8388	3313	3687	5503	11487	14265
No. 1+ animals	2312753	2145031	2066806	1932953	1823934	1768570	1743757	1597515	1554184	1532589	1556169	1335783

TABLE 5 (*Concluded*)

Age	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
0	444307	343878	373190	458617	412971	445669	420976	380759	350972	313938	358976	376386
1	134689	140497	129826	120212	144853	217369	174225	167317	138207	200129	183062	208804
2	150394	117814	118357	104921	96986	123598	174127	148044	142380	122381	176726	154267
3	139722	130017	101632	95797	88799	82266	107454	148249	129748	125823	106481	152368
4	110721	118656	111382	85786	83626	76333	70485	83313	129829	113623	109894	93003
5	100392	91774	99819	94267	74569	72894	65736	60394	82161	114355	99410	96399
6	76516	84509	74434	83510	80723	64946	62238	56398	52706	71793	98854	86862
7	77792	60997	68462	60666	70016	70409	55942	53939	49600	46044	62884	85233
8	47790	65522	51477	56011	50029	60171	60482	48237	47555	43482	39856	55179
9	42732	39412	56737	42584	47086	42279	50870	52419	42528	41721	37493	34429
10	34860	35116	34144	48718	35892	40403	35528	43458	46038	37323	36050	32242
11	36749	26617	29893	28644	41741	30365	34320	29851	37985	40283	32322	31265
12	27010	30337	23130	24290	23403	36006	25520	29408	26111	33333	34628	28148
13	32513	21697	25096	18979	20190	19907	31038	21512	25667	22738	28457	30055
14	30145	27099	18736	20844	15692	17093	16539	26584	18732	22380	19132	24612
15	48465	25019	22712	14993	16849	12836	13992	13960	23458	16378	18964	16424
16	36942	40599	20987	18805	11668	14011	10138	11341	12140	20543	13606	16284
17	14999	30776	35475	17233	15561	9431	11566	8182	9838	10545	17471	11492
18	36970	10656	26977	30610	13522	13032	7236	9520	7032	8529	8764	15028
19	15408	28935	8709	22541	25809	10896	10646	5720	8157	6063	7022	7398
20	31873	11546	24909	6793	18598	22014	8738	8835	4867	7129	4913	5909
21	15879	28305	9981	21192	4981	15889	18767	7158	7579	4104	5826	4095
22	27488	12100	24895	8169	18263	3986	13535	16878	6195	6638	3381	4932
23	18479	23455	10530	21705	6825	15649	3034	11782	14343	5439	5271	2745
24	6920	15421	20873	8747	18845	5732	13499	2532	10296	12734	4663	4512
25	33551	4648	13677	18272	7427	16562	4862	11861	2137	9136	11220	3954
No. 1+ animals	1328999	1221524	1062850	1074289	1031953	1094077	1080517	1076892	1075289	1142646	1166351	1205640

fisheries, should give the most reliable pup production following the application of a maturity ogive. These pup productions, resulting from determining the breeding population, are probably more reliable than those predicted from sequential analysis. However, the number of animals in age-groups older than 1 should be equivalent to the sequential analysis estimates. Recruitments to the 2+ populations were the cohort analysis abundance estimates for 1 yr olds.

The sex ratio of the catch was distributed over ages in accordance with the asymptotic function appearing in Fig. 1. The value of the asymptote is represented by the fraction of males in the catch (Table 6). For 2 yr olds, the percentage of females remained 52.8%; however, the asymptotic ratio varied in relation to the closing dates of the seal hunt.

In 1961 the sex ratio was assumed to be 50:50 in the population, changing thereafter in response to the sex ratio of the hunt on the molting patches and the contribution of this hunt to the total catch of 1+ seals (Table 5). This assumption is reasonable since the number of adult females taken by large vessels on the breeding patches during the postwar period was small because the value of whitecoat pelts was 2–6 times that of an adult pelt. Annual prices for the Norwegian fishery are given by Fiskeridirektøren (1951–65). Prior to this time Coleman (1938) suggested that few adult females were taken in the steamboat fishery since the cost of powder and shot was in excess of the value of the pelt. From 1895 to 1923 adult seals comprised only 2.7% of the total steamboat catch (Chafe et al. 1923). Even less of this would be females. From 1953 to 1960 whitecoats were worth from 1.3 to 2 times as much as the adults; however, this declined to 0.7 by 1964. Furthermore, due to the labor associated with skinning and transporting the adult pelts, it is unreasonable to assume that there was excessive killing of breeding females when whitecoats were available.

To protect the mature females a closing date of May 5 was established in the Gulf and on the Front in 1961. At this time we assume the sex ratio in the large vessel catch was 55% adult males since the sex ratio in the population would probably be altered in favor of females. Since the proportion of molting females on the ice would be less than males, the fraction of females in the catch would also have been somewhat smaller than the fraction of males. In 1963 the closing date was changed to April 30. The closing date in 1965 in the Gulf was altered to April 25, and this date was also established on the Front in 1968. In 1970 the closing date was April 29 and since 1971 it has been April 24. An agreement was made in 1965 that no females could be killed while breeding.

These regulations obviously decreased the percentage of mature females in the catches. The total Norwegian sample of molting harp seals taken from 1969 to 1974 (Benjaminsen and Øritsland 1975) showed a marked surplus of males. In age-groups 1 and 2 the sex ratio is approximately 50:50 and thereafter increases to 86% males for mature animals (Fig. 1). This was not the case in 1976. The proportion of adult females in the main patch was suspiciously high. Possibly this was due to the availability of *Pandalus borealis* being greater in the area occupied by the molters (Bergfløt 1976).

The projection is broken down into males and females and each sex is handled separately in the simulation (Table 6). The fertility rate was assumed to be about 94% during this period, and 6% of the breeding population was assumed to be over the age of 25 (Benjaminsen and Øritsland 1975). A constant, conservative maturity ogive, calculated from Sergeant's (1966, 1976) data was applied to the breeding population using the following schedule:

Age	Fraction whelping
2	0
3	0.075
4	0.220
5	0.450
6	0.700
7	0.880
8	0.970
9	0.990
10	1.000

The sex ratio in the breeding population became as high as 54.9% in favor of females in 1971, and has continually dropped since then to 52.9% in 1976 (Table 6) as a result of a much reduced hunt for molting animals (Table 2). Age-specific sex ratios rise as seals get older due to the accumulated effect of selective hunting. In fact, in more recent years this ratio has exceeded 70% females for animals over 20 yr.

The change in the sex ratio provides for more pups than would be calculated by applying a 50:50 ratio. Indeed, it is assumed that pup production calculated in this manner is more reliable than that estimated from sequential analysis (Fig. 3). Production reached a minimum in 1972 of 294,071 animals, down from the 424,561 produced in 1962. Since 1972 the production has slowly increased, primarily due to the entry of the 1968 year-class and the quota regulations, so

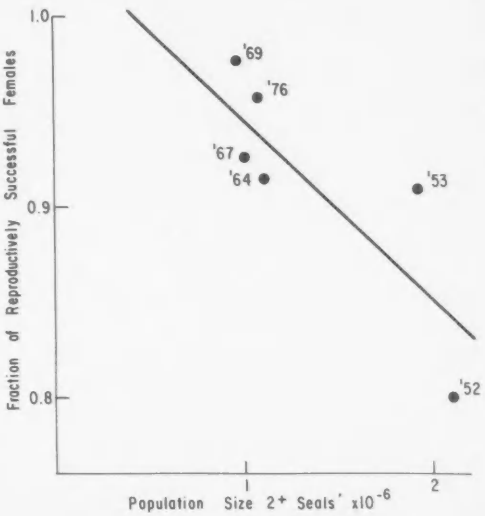

FIG. 5. The decline in northwest Atlantic female harp seals that have reproduced successfully in relation to population size.

that currently production would be 311,502. Using Sergeant's latest (1976) maturity estimates, production would now be approximately 330,000.

DIRECT SURVEY METHODS

Ultraviolet sensing method — Ultraviolet photography has been used for detecting certain white animals against a white background of ice or snow (Lavigne and Øritsland 1974). This method could significantly improve estimates of harp seal pup production. Details of this method have been outlined by Lavigne et al. (1975), as it was applied to the northwestern Atlantic harp seal. It is stated that using a direct statistical method, i.e. applying a mean density estimate to the total herd area, results in confidence limits much too large to suggest the method is useful. In addition, the patchiness of seals on the ice results in a skewed distribution from the subplot estimates such that the modal value is indeed much less than the mean.

Lavigne et al. (1975) have suggested that a ratio estimate should be used to reduce the confidence limits of the estimate. This method requires additional information over that needed for a direct estimate. Furthermore, the assumptions concerning these supplementary data are critical to the estimate. For this method to improve upon the direct estimate, the correlation of the number of adults to pups in the subplots must be greater than the ratio of the coefficient of the variance of adults among the subplots divided by 2 times the coefficient of variance of the number of pups among subplots. Lavigne et al. (1975) counted the number of adults from 1220 m to get an estimate of the total herd size and determined ratio estimates at 305 m.

It is suggested that their sample size of 69 subplots was too small. However, this required a correlation coefficient, r_{AP}, of only 0.232 between pups and adults for the method to be valid. Thus the minimum assumption required for the method to be valid is

$$\frac{\sigma_A^2 \times P}{2\sigma_P^2 \times A} = 0.232$$

where σ^2 is the variance among subplots of pup abundance, P, and adult abundance, A. This, of course, is a minimum assumption and is subject to change depending on how good the actual agreement is between the number of pups and adults. This method, although perhaps the most promising of all, requires counts of pups on the ice to compare with aerial counts, or ground truthing, and a more thorough knowledge of the stratification of the different ice types on which pups are found. Until these objectives are achieved it cannot be considered an adequate method, useful in the evaluation of the status of the harp seal stock.

Curran's survey method — Currently, there is only one method of direct estimation of pup production which some scientists agree upon as being reliable (Fig. 3). Perhaps our confidence in it is more because of the man and his long years of experience with seal management than with the technique. The following is a brief description of the method:

On March 8 and 9 a grid is flown from northern Labrador to Notre Dame Bay, Newfoundland, to locate the herd. The position of whelping patches depends on the area of most abundant food supply and the formation of rather loose, light, rough ice interspersed with sufficient leads of water. At this time the younger females, which have less control of parturition than older seals, are hauling up on the ice to give birth. The sighting of these younger animals gives the herd's location. The older females remain in the area of abundant food and approximately 2 days later will begin to whelp in a somewhat more northerly location since the younger animals will have drifted about 30 miles to the south. This usually gives the appearance of two herds. The majority of the Front herd has whelped by March 12 (T. Curran, Goose Bay, Labrador, personal communication).

Each of these two herds is surveyed separately.

TABLE 6. Projected populations of male and female northwest Atlantic harp seals, and age-specific sex ratios starting from 1961. The sex ratio of the large vessel catch was determined empirically, while the sex ratio of the landsmen's catch was considered to be that of the population. A maturity ogive was applied to calculate the breeding stock size.

	1962			1963			1964			1965			1966			1967		
Age	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀
1	107566	107566	50.00	87866	87866	50.00	67345	67345	50.00	70249	70249	50.00	64913	64913	50.00	60106	60106	50.00
2	93245	93245	50.00	84090	84090	49.99	75864	74864	49.99	59040	59033	50.00	59649	59646	50.00	53005	52998	50.00
3	71465	71465	50.00	68484	68484	49.99	71746	71743	49.99	65837	65826	50.00	51174	51156	50.00	48815	48792	49.99
4	55941	55956	50.01	59542	59660	50.05	57990	58204	50.09	61260	61415	50.06	56654	56813	50.07	43342	43554	50.12
5	55729	55765	50.02	45695	45925	50.13	51154	51482	50.16	48383	49042	50.34	51829	52381	50.26	47999	48638	50.33
6	34253	34273	50.01	46552	46811	50.14	39055	39541	50.31	43162	43901	50.42	39434	41037	51.00	43315	44667	50.77
7	31154	31185	50.02	29235	29384	50.13	39578	40307	50.46	31089	32562	51.16	34849	36819	51.37	32020	34604	51.94
8	26045	26090	50.04	26444	26617	50.16	24131	24950	50.83	33258	34557	50.96	26205	28032	51.68	28084	31281	52.68
9	27458	27490	50.03	21821	22047	50.26	21564	22528	51.09	19768	21149	51.69	28845	30167	51.12	21267	24113	53.14
10	20400	20428	50.04	23125	23352	50.24	17590	18565	51.35	17573	19086	52.06	17109	18515	51.97	24588	27351	51.73
11	23260	23321	50.07	17587	17682	50.14	18479	19564	51.43	13174	15090	53.39	14830	16632	52.86	14112	16034	53.19
12	22148	22183	50.04	20079	20227	50.18	13602	14546	51.68	15135	16625	52.35	11444	13239	53.64	11707	14220	54.85
13	33214	33226	50.01	18793	18976	50.24	16379	17136	51.13	10806	12170	52.97	12332	14297	53.69	9128	11401	55.53
14	25747	25761	50.01	29103	29182	50.07	15131	15995	51.39	13568	14635	51.89	9376	10583	53.02	10012	12355	55.24
15	12019	12041	50.04	22254	22371	50.13	24291	25049	50.77	12470	13631	52.22	11245	12649	52.94	7255	9002	55.37
16	25071	25074	50.00	9657	9816	50.41	18541	19161	50.82	20170	21502	51.60	10368	11763	53.15	9101	10904	54.51
17	11583	11601	50.04	21998	22048	50.05	7036	7840	52.71	15309	16386	51.70	17583	18950	51.87	8804	10099	54.88
18	21264	21279	50.02	9478	9633	50.41	18526	19012	50.65	4737	6109	56.33	13406	14455	51.88	15022	16635	52.55
19	11107	11114	50.02	18551	18622	50.10	7740	8174	51.36	14202	15686	52.48	3744	5241	58.33	10937	12546	53.43
20	18711	18722	50.01	9606	9659	50.14	15978	16262	50.44	5664	6575	53.72	12143	13738	53.08	2703	4434	62.13
21	12238	12245	50.00	16010	16124	50.18	7973	8241	50.83	14197	14449	50.44	4870	5772	54.24	10152	12010	54.19
22	5176	5176	50.00	10835	10835	50.04	13767	14077	50.56	5931	6695	53.02	12334	12741	50.81	3855	4977	56.35
23	21523	21531	50.01	4287	4334	50.27	9271	9434	50.44	11677	12217	51.13	5131	5904	53.50	10798	11279	51.09
24	8100	8103	50.01	19177	19184	50.01	3502	3654	51.06	7666	8073	51.29	10396	10876	51.13	4148	5114	55.22
25	5771	5771	50.00	7143	7158	50.05	16850	16954	50.15	2249	2778	55.26	6805	7168	51.30	9038	9625	51.57
Fraction ♂ in catch	0.550			0.550			0.65			0.65			0.75			0.75		
Fraction ♀	0.500			0.501			0.405			0.509			0.511			0.517		
Fraction ♀ in breeding pop.	0.500			0.502			0.508			0.516			0.519			0.528		
Breeding pop. size	424561			404631			384887			356267			350906			338231		

TABLE 6 (*Continued*)

	1968			1969			1970			1971			1972			1973		
Age	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀
1	72427	72427	50.00	108685	108685	50.00	87113	87113	50.00	83659	83659	50.00	69104	69104	50.00	100065	100065	50.00
2	48961	48947	50.00	62195	62189	50.00	88146	88097	49.99	74493	74467	49.99	71782	71766	49.99	61388	61369	49.99
3	45115	45081	49.98	41856	41826	49.98	54241	54217	49.99	75554	75461	49.97	65503	65458	49.98	63512	63453	49.98
4	42689	42716	50.02	38904	39078	50.11	35964	36097	50.09	47232	47291	50.03	65344	66365	50.01	58045	57983	49.97
5	37710	38025	50.21	37241	37480	50.16	33530	33932	50.30	30882	31225	50.28	41646	41780	50.08	58486	58512	50.01
6	41074	42066	50.60	32786	33422	50.48	31703	32466	50.59	28808	29407	50.51	27004	27429	50.39	36800	36924	50.08
7	36187	38221	51.37	35747	37044	50.89	28074	29208	50.99	27426	28433	50.90	25353	25990	50.62	23744	24104	50.42
8	26253	29459	52.88	30835	33574	52.13	30442	32416	51.57	24019	25621	51.61	24171	25194	51.04	22360	22992	50.70
9	23353	26994	53.62	21837	25840	54.20	25606	29348	53.40	26296	28432	51.95	21159	22707	51.76	21296	22256	51.10
10	17761	20814	53.96	19742	23794	54.65	17981	22599	55.69	21707	25632	54.15	23025	25198	52.25	18723	20137	51.82
11	20931	22946	52.30	14717	18273	55.39	16476	20825	55.83	14976	19610	56.70	18916	22666	54.51	20370	22341	52.31
12	11272	13663	54.79	17831	20253	53.18	12087	15944	56.88	14003	18214	56.54	13068	17356	57.05	16580	19931	54.59
13	9546	12238	56.18	9417	11993	56.02	15182	17826	54.00	10012	13897	58.13	12164	16107	56.97	11389	15231	57.22
14	7402	9783	56.93	7882	10761	57.72	7563	10449	58.01	12864	15615	54.83	8680	12268	58.56	10713	14235	57.06
15	7864	10499	57.17	5790	8541	59.60	6137	9373	60.43	6263	9110	59.26	11339	13854	54.99	7465	10656	58.81
16	5412	7536	58.20	6317	9188	59.26	4245	7367	63.44	4769	8067	62.85	5411	8043	59.78	9926	12199	55.14
17	7378	9362	55.93	4154	6556	61.21	4988	8011	61.63	3265	6339	66.00	4092	7128	63.53	4723	7094	60.03
18	6222	8509	57.76	6009	8195	57.69	2872	5632	66.23	3974	6924	63.54	2755	5592	66.99	3485	6203	64.03
19	12444	14434	53.70	4720	7419	61.12	4653	7144	60.56	2093	4849	69.85	3334	6109	64.70	2266	4795	67.91
20	8781	10789	55.13	10383	12727	55.07	3488	6464	64.96	3741	6203	62.38	1722	4276	71.30	2887	5355	64.98
21	1741	3644	67.67	7331	9527	56.51	8615	11224	56.58	2731	5589	67.18	3148	5472	63.48	1248	3540	73.95
22	8651	10536	54.91	1229	3181	72.13	6074	8395	58.02	7457	9923	57.09	2317	4947	68.10	2642	4709	64.06
23	3143	4315	57.86	7261	9302	56.16	708	2760	79.59	5230	7422	58.66	6468	8815	57.68	1954	4314	68.83
24	9292	9932	51.66	2546	3801	59.89	6129	8236	57.33	531	2412	81.98	4521	6590	59.31	5728	7825	57.74
25	3473	4447	56.15	8108	8829	52.13	2081	3357	61.74	5354	7302	57.70	391	2134	84.54	3964	5819	59.48
Fraction ♂ in catch	0.75			0.86			0.86			0.86			0.86			0.86		
Fraction ♀	0.520			0.521			0.524			0.524			0.522			0.518		
Fraction ♀ in breeding pop.	0.534			0.541			0.549			0.549			0.545			0.538		
Breeding pop. size	321977			315332			302092			296103			294071			299838		

TABLE 6 (*Concluded*)

Age	1974			1975			1976			1977		
	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀	♂	♀	% ♀
1	91531	91531	50.00	104402	104402	50.00	73598	73598	50.00	79888	79877	50.00
2	88545	88539	50.00	77800	77733	49.98	88916	88760	49.96	61790	61619	49.93
3	53788	53656	49.99	76733	76697	49.99	66909	66743	49.94	77242	77002	49.92
4	55636	55739	50.05	46964	47090	50.07	66984	66982	50.00	58269	58097	49.93
5	50844	51096	50.12	48811	49142	50.17	40965	41165	50.12	58725	58724	50.00
6	50507	51322	50.40	44389	44987	50.33	42565	42978	50.24	35969	36176	50.14
7	32220	32616	50.30	43466	44838	50.78	38682	39393	50.46	37512	37898	50.26
8	20512	21158	50.77	28255	28796	50.47	37919	39231	50.85	34100	34785	50.50
9	19217	20199	51.25	17704	18502	51.10	24628	25214	50.59	33440	34653	50.89
10	18425	19489	51.40	16424	17703	51.87	15390	16253	51.37	21779	22345	50.64
11	16219	17666	52.14	15938	17117	51.78	14240	15459	52.05	13449	14233	51.42
12	17536	19515	52.67	14087	15553	52.47	13846	15045	52.08	12507	13612	52.12
13	14209	17335	54.95	15151	17185	53.15	12256	13648	52.69	12212	13299	52.13
14	9610	13212	57.89	12215	15261	55.54	13179	15095	53.39	10808	12083	52.78
15	9100	12352	57.58	8190	11617	58.65	10625	13417	55.81	11638	13365	53.45
16	6166	9192	59.85	7734	10860	58.41	7111	10247	59.04	9287	11792	55.94
17	8431	10620	55.74	5135	8011	60.94	6710	9567	58.78	6265	9084	59.18
18	3892	6134	61.18	7192	9323	56.45	4436	7073	61.46	5897	8466	58.94
19	2815	5356	65.55	3212	5370	62.57	6248	8200	56.76	3900	6264	61.63
20	1746	4155	70.42	2291	4694	67.20	2774	4742	63.10	5522	7270	56.83
21	2273	4651	67.17	1377	3640	72.56	1972	4148	67.78	2418	4176	63.33
22	952	3093	76.47	1869	4080	68.58	1175	3222	73.28	1743	3689	67.91
23	2053	3982	65.99	682	2695	79.80	1601	3612	69.29	1027	2862	73.59
24	1612	3828	70.37	1710	3511	67.25	569	2392	80.80	1413	3211	69.45
25	5012	6966	58.16	1286	3391	72.51	1466	3106	67.94	497	2133	81.04
Fraction ♂ in catch	0.86			0.86			0.86			0.86		
Fraction ♀	0.517			0.516			0.514			0.512		
Fraction ♀ in breeding pop.	0.536			0.534			0.529			0.524		
Breeding pop. size	302165			305609			311502			319914		

First, the extensiveness of a herd is determined by circling it and drawing a parallel grid line. The grid is followed by aircraft and X's are marked on it where there are no seals so the total area of seal density can be calculated. The pups in specific subpatches are then counted by Curran and his crew for at least 8 ha. Each subpatch is about 0.4 ha in size and randomly distributed. In some areas the seals are scattered and in others dense, such that a mean number per hectare and an associated variance can be calculated. This survey is conducted from a helicopter and sealing vessels. The density is now applied to the subherd, for which the total area has been determined, to give the population size. This exercise then allows for visual estimates from the aircraft for the remaining herd. Norwegian and Canadian sealers will hunt off particular areas, and Curran receives daily counts of their take. When the hunters move out he will count the remaining seals and add this to the catch, thus arriving at total figures for different areas. By relating these figures to his own estimates he can get an idea of how accurate his original estimates were. In addition to soon learning what a specific number of pups looks like from the air, he claims his method of estimation is always conservative by at least 10%; this is possibly an overstatement.

There is no doubt the method is crude and could be improved by good aerial photography. However, because of his efforts in ground truthing, his direct estimates are perhaps the most accurate available.

It has been proposed that ⅓ of the seal herd whelps in the Gulf and ⅔ whelp on the Front (Sergeant 1976). According to Curran's estimates from 1971 to date, the breeding population on the Front is about 6% larger than that in the Gulf, when all factors are considered. Although Curran's estimates are conservative, the implications of this fact are serious. It means that, with the Gulf closed to hunting from large vessels, the Front could become severely overexploited. Apparently, the juvenile seals intermix between the two areas (Sergeant 1976), in addition to adults during years of poor ice condition. However, as a rule adults do not mix, and therefore there is a possibility the assumption that the two herds may be one (Sergeant 1965) is wrong.

Construction of simulation — It is our opinion that some further insights can be gained into the population dynamics of harp seals by the construction of a stochastic simulation. By stochastic it is meant that the distribution and variance of certain parameters and state variables are taken into account. Another assumption is that the Front and Gulf herds are indeed one population since they spend the summer together in the arctic (Sergeant 1965), and intermix as juveniles (Sergeant 1975). Of the two assumptions possible, more evidence supports the one herd hypothesis.

The simulations written in A Programming Language (APL) (Table 7) are represented by the schematic flow chart (Fig. 6). The program presented in Table 7 requires specific large vessel catches of 1+ seals and pups to be entered; however, the alternative program is slightly changed so fishing mortality rates rather than large vessel catches are entered.

To initiate the program a starting population of animals aged 1–25 is entered, then the number of years the program is to run, and the starting date. A quota can then be set by entering in a large vessel catch of 1+ seals and pups. An option is also available whereby the catch of 1+ seals and pups by the Magdellanot can be fixed.

The simulation has two options related to its printout. If the number of runs is deemed as one, it will print out the breeding and total population size, the annual sex ratio of the total and breeding population, and the total catch of 1+ seals and pups. However, since the model is stochastic, each run will give different answers since the "seed" in the random number generator is not fixed for each iteration. Thus, when the number of runs is greater than one, matrices of total annual and breeding population, in addition to the catch of 1+ seals and pups, are printed out. The right-hand two columns in each of the matrices are the mean and standard deviation for that year.

The starting population is now broken up into the male and female fractions present in 1977 (Table 7, [34][2]). One of the problems with this fishery that does not allow it to be interpreted accurately using conventional fisheries models is that the frequency distribution of the catch bears little relationship to the frequency distribution of the population. Therefore, the catch cannot be distributed in a similar structure to the population. The frequency distributions of four district fisheries (Fig. 7) are used: the high arctic, Greenland, landsmen's, and large vessel catches. The distributions are averages over a number of randomly chosen years between 1952 and 1975 so that biases due to trends in recruitment and effort are reduced. The interpolated values from the curves of best fit were entered into the simulation as average constant values representing the catch frequencies (Table 7 [45]–[52]).

[2][*n*] represents the line in the program in Table 7.

TABLE 7. Program listing of APL simulation of northwestern Atlantic harp seal.

```
      VHARP[□]V
   ∇  HARP
[1]    'STARTING POP ONE AND OLDER'
[2]    POP1←POP←□
[3]    'NUMBER OF YEARS'
[4]    X←□
[5]    'ENTER FIRST YEAR'
[6]    DAY←DATE←□
[7]    'LARGE VESSEL CATCH'
[8]    LVC←□
[9]    'PUP CATCH'
[10]   PC←□
[11]   'MAGDALEN QUOTA ON PUPS'
[12]   MPQ←□
[13]   'MAGDALEN QUOTA ON ONE PLUS'
[14]   MAQ←□
[15]   'NUMBER OF RUNS'
[16]   Z←□
[17]   STAR←0
[18]   BPOP←YEAR←TPOP←TSEX←BSEX←TCA
       ←TCP←⍳0
[19]   →START
[20] TAKEOFF:→(QM<23.58)/BACK
[21]   MAT← 0 0 0.16 0.4 0.68 0.89 0.97 ,(18⍴1)
[22]   →AA
[23] FIX1:QM←0
[24]   →LETT
[25] FIX2:QM←90
[26]   →LETT
[27] AAAA:BREED←0
[28]   →ABC
[29] BBBB:TOTALP←0
[30]   →BCD
[31] START:STAR←STAR+1
[32]   POP←POP1
[33]   DATE←DAY
[34]   CR← 0.5 0.4993 0.4992 0.4993 0.4999 0.5014
       0.5026 0.505 0.5089 0.5064 0.5142 0.5211 0.5213
       0.5278 0.5345
[35]   CR←CR, 0.5594 0.5918 0.5894 0.6163 0.5683
       0.6333 0.6791 0.7359 0.6945 0.8104
[36]   FPOP←POP×CR
[37]   MPOP←POP−FPOP
[38]   →AROUND
[39] GO1:PREG←1
[40]   →SKIP
[41]   XX←0
[42] AROUND:XX←YY←0
[43] GO2:XX←XX+1
[44]   DATE←DATE+1
[45]   CORR← 0.528 0.528 0.591 0.645 0.693 0.731
       0.764 0.79 0.811 0.826 0.838 0.846 0.851
       0.853 ,(11⍴0.854)
[46]   PLV← 0.3071 0.14 0.077 0.0602 0.049 0.042
       0.0364 0.0328 0.0294 0.0272 0.0246 0.0227 0.021
       0.0196 0.0182
[47]   PLV←PLV, 0.0174 0.0154 0.0134 0.0126 0.0101
       0.0076 0.0067 0.005 0.0042 0.0006
[48]   PLC← 0.1187 0.107 0.0978 0.0877 0.0781 0.0701
       0.0618 0.0544 0.048 0.0424 0.0369 0.0323 0.0277
       0.024 0.0207
```

TABLE 7 (*Continued*)

```
[49]   PLC←PLC, 0.01077 0.0151 0.0129 0.0109 0.0092
       0.0076 0.0063 0.0052 0.0041 0.0031
[50]   PGC← 0.3059 0.1851 0.1253 0.0839 0.0575
       0.0425 0.031 0.0241 0.0184 0.0149 0.0126 0.0108
       0.0097 0.0086 0.0078
[51]   PGC←PGC, 0.0074 0.0069 0.0067 0.0063 0.0061
       0.0059 0.0057 0.0056 0.0055 0.0054
[52]   PNC← 0.1312 0.1602 0.2123 0.1158 0.083 0.0617
       0.0463 0.0367 0.0289 0.0232 0.0183 0.0154 0.0125
       0.0104 0.0085
[53]   PNC←PNC, 0.0071 0.0058 0.005 0.0042 0.0034
       0.0031 0.0027 0.0023 0.0019 0
[54]   MLVC←LVC×PLV×CORR
[55]   FLVC←(LVC×PLV)−MLVC
[56]   →(MAQ>0)/YYY
[57]   LC←(5048×((+/((12?1000)÷1000))−6))
       +13026
[58]   →BBB
[59] YYY:LC←((5051×((+/((12?1000)÷1000))−6))
       +12451)+MAQ
[60] BBB:PF←FPOP÷(FPOP+MPOP)
[61]   FLC←PF×PLC×LC
[62]   MLC←(PLC×LC)−FLC
[63]   GC←(1040×((+/((12?1000)÷1000))−6))+3784
[64]   FGC←PF×PGC×GC
[65]   MGC←(PGC×GC)−FGC
[66]   NC←(729×((+/((12?1000)÷1000))−6))+1294
[67]   FNC←PF×PNC×NC
[68]   MNC←(PNC×NC)−FNC
[69]   POPU←+/(¯24↑POP)
[70]   PREG←(1.048−(0.097458×1E¯6×POPU))
[71]   →(PREG>1)/GO1
[72] SKIP:AGE←⍳25
[73]   M←(15.5223×AGE)+(¯2.245E¯5×(+/POP))
       +(¯16.01743)
[74]   MAT←⍳0
[75] GOTO:YY←YY+1
[76]   QM←1↑M
[77]   →(YY=4)/TAKEOFF
[78] BACK:→(QM<0)/FIX1
[79]   →(QM>90)/FIX2
[80] LETT:QM←1○(QM÷57.296)
[81]   MAT←MAT,QM
[82]   M←↓M
[83]   →(YY<25)/GOTO
[84] AA:PUP←BREEDPOP
       ←(+/(FPOP×PREG×MAT))×1.06
[85]   YY←0
[86]   FPOP←FPOP−(FLVC+FLC+FGC+FNC)
[87]   MPOP←MPOP−(MLVC+MLC+MGC
       +MNC)
[88]   TAC←+/(FLVC+FLC+FGC+FNC
       +MLVC+MLC+MGC+MNC)
[89]   →(MPQ>0)/XX
[90]   LPC←(14442×((+/((12?1000)÷1000))−6))
       +36949
[91]   →AAA
[92] XXX:LPC←((13998×((+/((12?1000)÷1000))−6))
       +24177)+MPQ
[93] AAA:GPC←(1040×((+/((12?1000)÷1000))−6))
       +3784
[94]   PUP←PUP−(PC+LPC+GPC)
```

TABLE 7 (*Continued*)

```
[95]   TPC←PC+LPC+GPC
[96]   NMORT←(0.0302×((+/((12?1000)÷1000))−6))
       +0.114
[97]   FPOP←FPOP×(*(−NMORT))
[98]   MPOP←MPOP×(*(−NMORT))
[99]   PUP←PUP×(*(−NMORT))
[100]  ONE←PUP÷2
[101]  FPOP←ONE,24↑FPOP
[102]  MPOP←ONE,24↑MPOP
[103]  POP←FPOP+MPOP
[104]  BREED←⌊(+/BREEDPOP)
[105]  →(BREED<0)/AAAA
[106]ABC:BPOP←BPOP,BREED
[107]  TOTALP←⌊(+/POP)
[108]  →(TOTALP<0)/BBBB
[109]BCD:TPOP←TPOP,TOTALP
[110]  SEXRT←⌊(((+/FPOP)÷(+/POP))×100)
[111]  SEXRB←⌊(((+/(FPOP×MAT))
       ÷(+/POP×MAT))×100)
[112]  TCA←TCA,TAC
[113]  TCP←TCP,TPC
[114]  TSEX←TSEX,SEXRT
[115]  BSEX←BSEX,SEXRB
[116]  YEAR←YEAR,DATE
[117]  →(XX<X)/GO2
[118]  →(Z≠1)/GO3
[119]  DATA←⌊(φ(7,X)ρ(YEAR,BPOP,TPOP,TSEX,
       BSEX,TCA,TCP))
[120]  DATA
[121]  →0
[122]GO3:→(Z>STAR)/START
[123]  BPOP←⌊φ((Z,X)ρBPOP)
[124]  TPOP←⌊φ((Z,X)ρTPOP)
[125]  TCA←⌊φ((Z,X)ρTCA)
[126]  TCP←⌊φ((Z,X)ρTCP)
[127]  X←Z
[128]  MBPOP←(+/[2] BPOP)÷X
[129]  SDBPOP←(((+/[2]((BPOP)*2))
       −(Z×(MBPOP*2)))÷(Z−1))*0.5
[130]  MATBPOP←BPOP,MBPOP
[131]  MATBPOP←⌊(MATBPOP,SDBPOP)
[132]  MTPOP←(+/[2] TPOP)÷X
[133]  SDTPOP←(((+/[2]((TPOP)*2))
       −(Z×(MTPOP*2)))÷(Z−1))*0.5
[134]  MATTPOP←TPOP,MTPOP
[135]  MATTPOP←⌊(MATTPOP,SDTPOP)
[136]  MTCA←(+/[2] TCA)÷X
[137]  SDTCA←(((+/[2]((TCA)*2))
       −(Z×(MTCA*2)))÷(Z−1))*0.5
[138]  MATTCA←TCA,MTCA
[139]  MATTCA←⌊(MATTCA,SDTCA)
[140]  MTCP←(+/[2] TCP)÷X
[141]  SDTCP←(((+/[2]((TCP)*2))
       −(Z×(MTCP*2)))÷(Z−1))*0.5
[142]  MATTCP←TCP,MTCP
[143]  MATTCP←⌊(MATTCP,SDTCP)
[144]  '                TOTAL POPULATION'
[145]  MATTPOP
[146]  ''
[147]  ''
[148]  '                BREEDING POPULATION'
```

TABLE 7 (*Concluded*)

```
[149]  MATBPOP
[150]  ''
[151]  ''
[152]  '                CATCH OF PUPS'
[153]  MATTCP
[154]  ''
[155]  ''
[156]  '                CATCH OF ADULTS'
[157]  MATTCA
       ∇
```

All the uncontrolled catches, i.e. those excluding large vessels, had a normally distributed random component. The means and standard deviations for these fisheries were as follows:

Catch of 1+ seals

Landsmen	13,026 ± 5,048	1 SD
Greenland	3,784 ± 1,040	(Kapel 1975)
High arctic	1,294 ± 729	(Sergeant 1971)

Catch of O-group seals

Landsmen	36,949 ± 14,442	1 SD
Greenland	3,784 ± 1,040	

In each case, the catch was broken into the frequency distribution through multiplying it by the average catch distribution. It was then fractioned into males and females by assuming that (1) each uncontrolled catch had the same sex ratio as the current population, and (2) the large vessel catch had the same age dependent sex ratio as that in Fig. 1 since the closing dates are to remain fixed.

The next step in the program is to calculate the size of the breeding population ([84]), and for this two functions must be evaluated:

First density-dependent, age-specific whelping ages are calculated using the equation ([73]):

$$\text{(I)} \quad \text{arc sine } {}_iE_t = 15.522A - 2.245 \times 10^{-5}N_t - 16.017$$

where ${}_iE_t$ is the fraction of the population whelping assuming 100% pregnancy for a particular age i and population number of 1+ seals N_t in the year t, and A is the age in years. The arc sine of ${}_iE_t$ is constrained such that it cannot be 90 or 0.

A density-dependent fertility rate is calculated using the following equation ([73]):

$$\text{(II)} \quad P = 1.-48 - 9.746 \times 10^{-8}N_2$$

where P is the pregnancy rate and N_2 is the number of harp seals between the ages 2 and 25. These two equations act together to constrain the pup production within the carrying capacity of

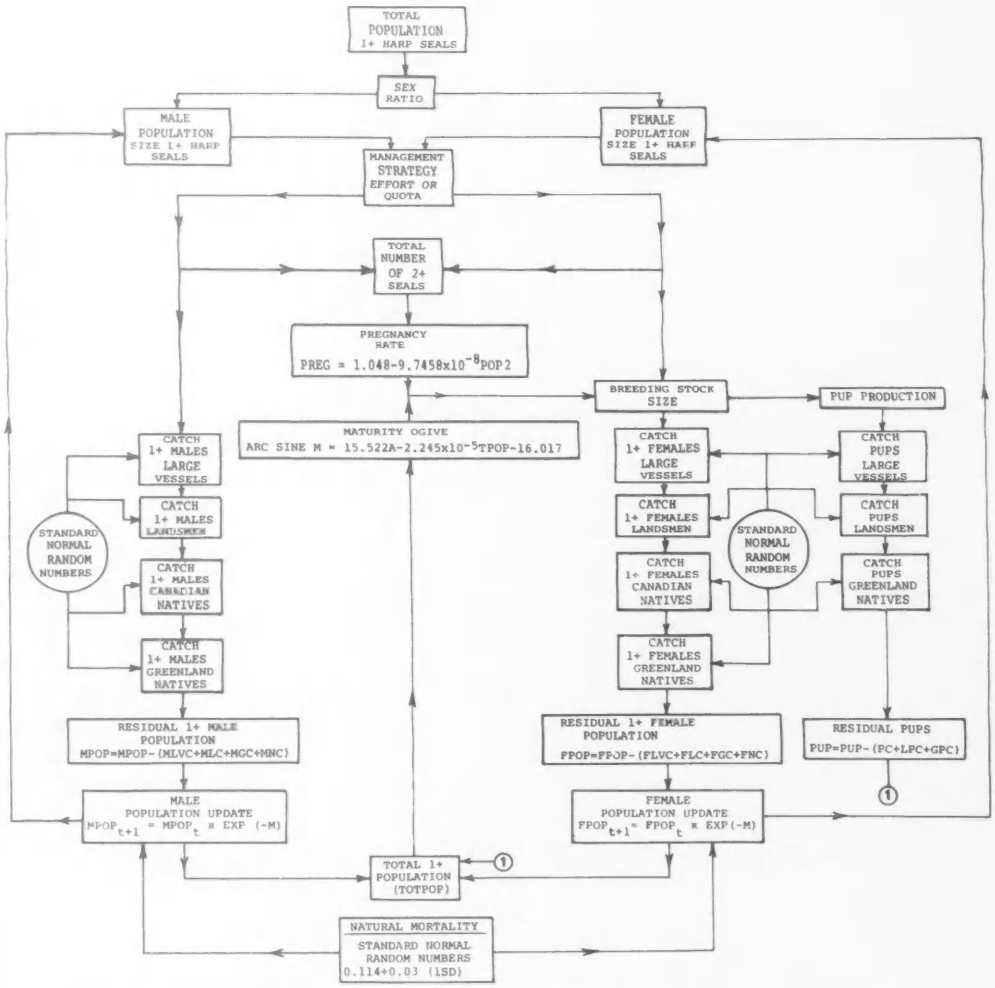

FIG. 6. Flow chart of the APL program simulating the northwest Atlantic harp seal.

the environment in addition to augmenting the production at lower population levels. They make the birth rate a power function of population size. The summation of the breeding population vector is multiplied by 1.06 since it was determined that on average 6% of the breeding population is over the age of 25.

Equations I and II represent the feedback within the simulation which changes its nature from linear to nonlinear, thus providing some additional realism.

Following the calculation of pup production the catches of 1+ males and females are subtracted from the total number ([86], [87]). Similarly, the pup catch is subtracted from the total catch ([94]).

Natural mortality is also considered a stochastic, normally distributed rate of 0.114 ± 0.0302 which means that it can vary as widely as from 0.174 to 0.0536, less than 5% of the time. Natural mortality is applied using the following equation ([97]–[99]):

$$\text{(III)} \quad N_t \leftarrow N_t \exp(-M)$$

Natural mortality is applied to the population after the catch has been subtracted, since the hunt

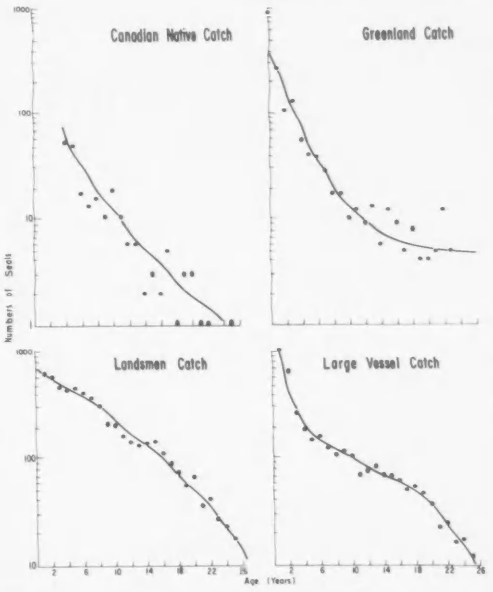

FIG. 7. Catch distribution from the different fisheries for the northwest Atlantic harp seal.

occurs primarily during the spring and natural mortality and hunting mortality occur quite separately.

The surviving pups after exploitation and natural mortality are assumed to have a 50:50 sex ratio. The numbers of males and females at age are now updated and the 0-group cohort is catenated into the vector for 1 yr olds and the remaining 25-yr-old seals are dropped from the vector ([101], [102]). Annual sex ratios of the total and breeding populations are calculated. A test is made to determine if the simulated time period has expired and if more iterations are to occur. If the simulation time has elapsed, the remaining portion of the program dealing with the calculation of means and variances and formating of output is executed.

Results and discussion of the simulation — Allen (1975) pointed out that his linear model allows the population to increase ad infinitum which restricts its usefulness for making long-term predictions. Thus the initial use of the simulation was to investigate the implications of different assumptions concerning the pregnancy and maturity rates on the population when there was no fishery other than the uncontrolled landsmen's and aboriginal hunts.

Many mammalian populations show a varying fertility rate (Gambell 1973; Markgren 1969) in response to space and food availability, and indeed there is evidence to indicate that the pregnancy rate for harp seals can also be altered in response to changes in density (Fig. 5). When this relationship was incorporated into the simulation, it limited the population (Fig. 8) to about 6.5 million animals. At this time the fertility rate was approximately 0.4 which brought the population into equilibrium with the uncontrolled landsmen's and aboriginal hunt. However, the reproductive potential of the stock was unrealistic, since when MSY, to be discussed later, was determined, catch levels could be sustained that were in excess of those that led to a decline in the herd.

It was apparent from this exercise that an additional mechanism was necessary to constrain the reproductive potential of the population. For this reason, a density-dependent maturity ogive was added to the simulation. The effect was to produce a population size in equilibrium with the landsmen's and aboriginal catch levels at an abundance of 3.7 million seals. Sergeant (1975) concluded that the 1952 population size was near the maximum; the sequential analysis estimate for 1952 (Table 5) was approximately 2.3 million seals. Evidence from this analysis does not agree

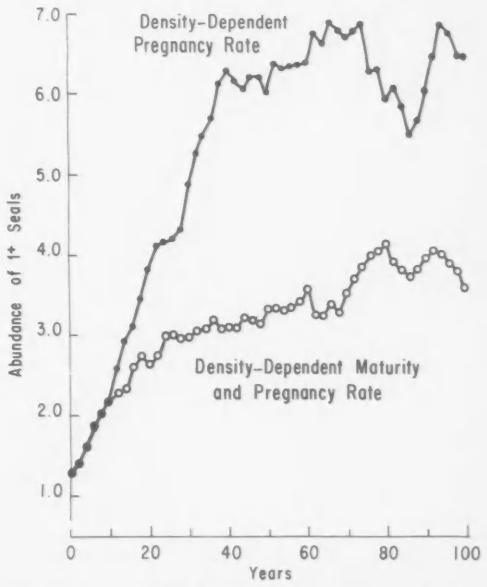

FIG. 8. Two simulated relationships showing the effects of density-dependent age of maturity and pregnancy rates on the northwest Atlantic harp seal.

with Sergeant's conclusions since the maximum population size was nearer 3.7 million.

A simulated "recruitment" curve (Fig. 9) was compared with values from the sequential population analysis. The line passed through the axis of the data, but the scatter in the pup production values was too great to suggest that the two techniques confirmed each another. However, one apparent fact was that pup production had to be in excess of the 1953 production level to sustain the high catches between 1880 and 1923 (Chafe et al. 1923).

The curve (Fig. 9) is a power function of population size. Allen (1975) speculates as to the possible shape of the recruitment curve and concluded that, if reproduction is a linear function of stock size, the Beverton and Holt (1957) recruitment curve is indeed the best representation of the recruitment process of seals. In addition to the linear shift in maturity, our model allows for a linear shift in the pregnancy rate which adds more curvature to the relationship. The so-called Ricker (1954) recruitment is not realistic for a stock as nondynamic as harp seals since the declining portion of this curve results from a population being much further out of equilibrium with the carrying capacity of the environment than is possible for seals to get. At the point of maximum population size then, the reproductive rate is equivalent to the mortality rate.

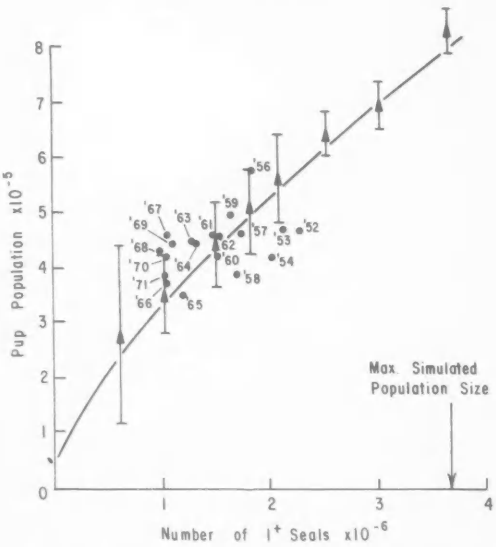

FIG. 9. Simulated recruitment curve and pup production from cohort analysis of the northwest Atlantic harp seal. Triangles are simulated values; dots are values from cohort anlysis; bars represent 2 SD

It was necessary to determine the MSY population level as a reference point for harp seal management. This could not be determined from the simulation if only catch were controlled since, under these conditions, the population could only come into equilibrium or collapse. Therefore, the alternate program was utilized such that catch would vary in response to population size by controlling the hunting mortality rate. This allows for a Schaefer-type curve (Fig. 10) to be generated. Hunting mortality by large vessels was calculated under present conditions to be approximately 0.01 on 1+ seals. Holding this mortality constant, the hunting level on pups was allowed to vary. The predicted value for maximum sustainable yield is approximately 200,000 pups and 40,000 1+ seals, with respect to the present pup to 1+ seals kill ratio. The MSY population size is near 1.6 million 1+ seals, or a breeding stock of 375,000 females.

The variance in catch becomes greater on the left-hand side of the Schaefer-type curve (Fig. 10). This fact has been speculated on by Doubleday (1976), but here the biological basis is apparent. At stock sizes less than 1.2 million, the maturity ogive can no longer shift to the left; thus, the population loses much of its density-dependent control to maintain stability. The same result was shown by Lett and Kohler (1976) for an Atlantic herring stock.

Using the 1977 age-specific abundance levels (Table 5) the population was projected ahead with fixed large vessel catches of pups and 1+

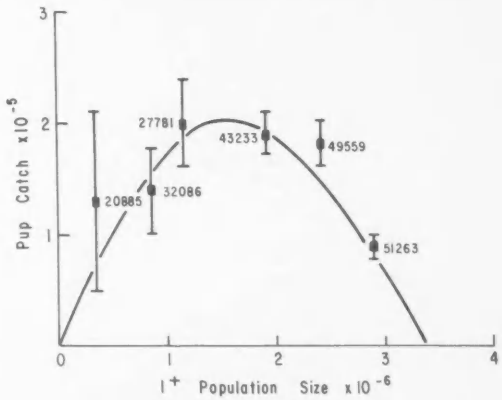

FIG. 10. Graham–Schaefer type curve illustrating the MSY population level of ~1.6 million for catch of pups and 1+ northwest Atlantic harp seals in their present proportions. Since lower catches of pups allow for large population sizes, a constant hunting mortality by large vessels will allow for a greater catch of 1+ seals. Bars represent 2 SD.

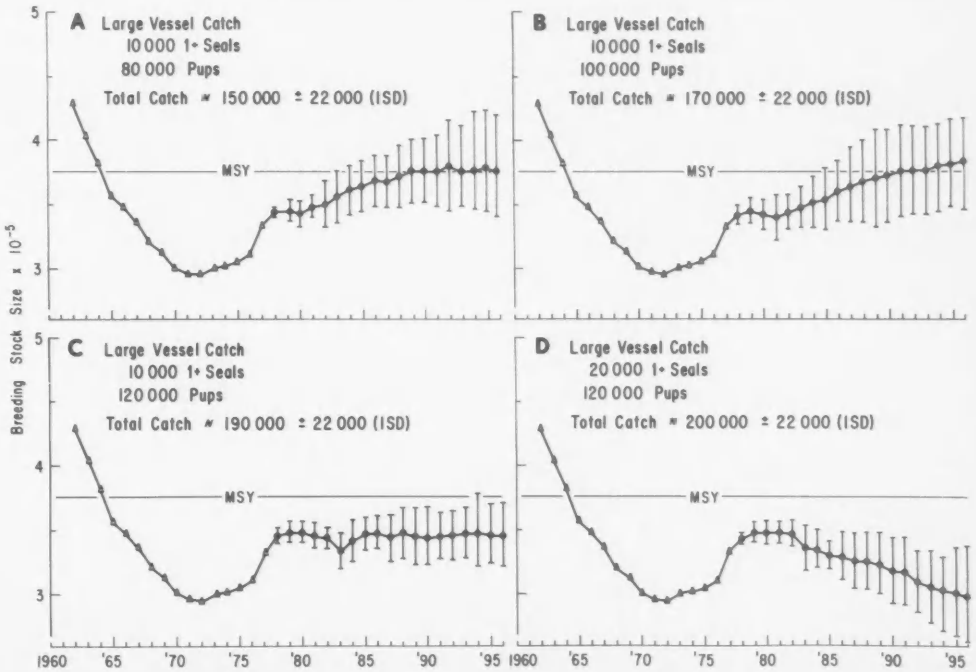

FIG. 11. Projected breeding stock of the northwest Atlantic harp seal in relation to varying management strategies. Confidence limits indicate we can put little reliance in projections further than 5 yr.

seals (Fig. 11). When the large vessels removed 10,000 1+ seals and 80,000 pups the mean population size increased, reaching the MSY breeding stock size by 1986; there is a 66% chance that MSY could be reached by 1983. The total average catch including seals caught by landsmen, sealers on large vessels, Canadian natives, and Greenlanders is ~150,000 seals. When the large vessels take 10,000 1+ seals and 100,000 pups the mean population size reaches MSY in 1991, a date not much different from that for the projected 1971–74 management strategy. In all iterations the population increased at this level of exploitation.

When the large vessel catch was 10,000 1+ seals and 120,000 pups for a total average catch of 190,000 the population size did not change. However, 20% of the time the population declined and 80% of the time it stayed the same or increased. When 10,000 more 1+ seals were removed by large vessels (Fig. 11D) the population declined in all cases.

In conclusion, this study indicates that the catch should not exceed 170,000 seals for 1977 to allow the population to increase to MSY, assuming a kill ratio of 20% 1+ seals to 80% pups and keeping in mind this total catch includes the high arctic and Greenland hunt. Furthermore, because of the growing uncertainties of prediction encountered as one moves away from the current population size (Fig. 11), quotas should not be set more than 3–5 yr in advance. A complete reexamination of the population dynamics and herd assessment is necessary at least every 5 yr.

Under a new management strategy for 1977, the landsmen's hunt will be restricted to a total kill of 63,000 seals. This quota will alter to some extent the philosophy behind setting the present TAC at 170,000 seals. At present, the landsmen's catch can be as high as ~90,000 seals. However, if the landsmen's hunt is still allowed to vary in relation to changing ice conditions but is truncated at a catch of 63,000 animals then the total overall TAC could be raised to 180,000 seals. This revised TAC depends on how well the new quota for landsmen can be enforced and should not be considered until after the 1977 sealing season.

Sampling of the landsmen's and large vessel catch must be continued at an accelerated level in the interim, in addition to samples collected from the molting lairs for estimates of natural mortal-

ity. Furthermore, samples of ovaries should be collected from the breeding females to detect shifts in the maturity ogive. Ultraviolet aerial sensing of the herd, with adequate ground truthing, must be pursued until a direct estimate of the population size is available. We believe that the model presented in this paper is complete as far as the population dynamics is concerned, and for this reason a logical extension of the simulation could incorporate some community structure and bioenergetic submodels.

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Piscine Erythrocytic Necrosis Virus in Atlantic Cod, *Gadus morhua*, and Other Fish: Ultrastructure and Distribution

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WALKER, R., AND S. W. SHERBURNE. 1977. Piscine erythrocytic necrosis virus in Atlantic cod, *Gadus morhua*, and other fish: ultrastructure and distribution. J. Fish. Res. Board Can. 34: 1188–1195.

Electron microscopy of erythrocytes of Atlantic cod, *Gadus morhua*, with piscine erythrocytic necrosis (PEN) shows a small cytoplasmic viroplasm (~1 μm), often with an adjacent coherent group of large (330 nm) icosahedral virions. The viroplasm is Feulgen-positive, so the agent is an erythrocyte icosahedral cytoplasmic deoxyribovirus (EICDV) analogous to others reported in red cells of poikilotherms. PEN lesions in cod blood cells were found in 11–16% of samples from New Brunswick, Maine, and Georges Bank. PEN was found in cod of 15–80 cm total length taken at depths of 5–90 m. Incidence in the Georges Bank area was higher at depths of about 55 m. Intensity of infection varied from <0.01 to ~99% of mature red cells, without obvious relation to cod size, sex, or condition, or to depth at which taken. PEN infections are reported in various other fish species and in other areas.

Key words: viral infections, cytology, ultrastructure, morphology, pathology, Atlantic coast fishes

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L'examen au microscope électronique d'érythrocytes de morues franches, *Gadus morhua*, atteintes de «nécrose érythrocytique des poissons» (NEP) indique un petit viroplasme cytoplasmique (~1 μm), souvent à proximité d'un groupe cohérent de grands (330 nm) virions icosaèdres. Le viroplasme est Feulgen-positif, de sorte que l'agent est un désoxyribovirus cytoplasmique icosaèdre de l'érythrocyte (DCIE) analogue à ceux qui ont été signalés dans les globules rouges des poïkilothermes. Nous avons observé des lésions dues à la NEP dans 11–16% des échantillons provenant du Nouveau-Brunswick, du Maine et du banc Georges. Nous avons trouvé la NEP dans des morues de 15–80 cm de LT capturées à des profondeurs de 5–90 m. L'incidence dans la région du banc Georges est plus élevée à des profondeurs d'environ 55 m. L'infection varie en intensité <0.01% à ~99% des globules rouges mûrs, sans qu'il y ait relation évidente avec la taille, le sexe ou l'état d'embonpoint de la morue; non plus qu'avec la profondeur à laquelle elle est capturée. Nous mentionnons des infections par la NEP chez diverses autres espèces de poissons et dans d'autres régions.

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PISCINE erythrocytic necrosis (PEN) was described in *Gadus*, *Liparis*, and *Myoxocephalus* by Laird and Bullock (1969), who suggested its viral nature. Walker (1971) reported electron microscopic (EM) evidence of icosahedral virus particles in the cytoplasm of cod red cells, and their maturation at the surface of the DNA-containing viroplasm. Sherburne (1973) reported cytoplasmic inclusions associated with erythrocytic degeneration in the Atlantic herring, *Clupea harengus harengus*; Philippon et al. (1977) report EM evidence that this herring infection is viral. Other EM of such PEN lesions in fish are given by Johnston and Davies (1973) for *Blennius*, and by Appy et al. (1976) for *Gadus*. Such icosahedral cytoplasmic deoxyriboviruses (ICDV) in erythrocytes of various cold-blooded vertebrates may be a significant subgroup of the ICDVs and are here designated EICDV. Stehbens and Johnston (1966)

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first gave EM evidence of such EICDV in lacertilian red cells with "Pirhemocyton" lesions, formerly attributed to a protozoan.

There has been renewed interest in other "doubtful protozoa" in red cells of various poikilotherms. Sousa and Weigl (1976) showed EICDV in Toddia lesions of a frog, and Bernard et al. (1969) had shown such particles in *Rana* erythrocytes after irradiation. Johnston (1975) showed large virus-like particles in Immanoplasma lesions of shark red cells, and he evaluated the literature. "Doubtful protozoa" in unexpected hosts, such as Pirhemocyton in turtles (Acholonu 1974) or Toddia in fish (Arcay de Peraza and McLure 1971), and other enigmatic inclusions (Peirce and Castleman 1974) call for EM check.

EM of EICDVs has scarcely contributed to understanding of life cycle or epidemiology. We have no reports of these EICDV in other tissues, and incidence data are from light microscopy of blood smears. As to transmission, only Pereira et al. (1973) have followed the time course after experimental blood inoculation of Toddia in anurans; slower changes occurred in milder normal infections; and some specificity was found between anuran genera.

The present report amplifies Walker's (1971) abstract and gives data on the incidence and distribution of PEN for Atlantic cod, *Gadus morhua*, and other species.

Materials and Methods

The 390 cod examined in this study ranged in total length from 12 to 80 cm and were taken from depths of 5 to 185 m. They included: (1) 256 cod from an area extending from 7 naut. miles off Chatham, Mass., to approximately 160 naut. miles offshore at the northeast tip of Georges Bank (October 24–29, 1972); (2) 116 cod from Maine waters, from Boothbay Harbor, Seguin and Monhegan islands, and St. John's Bay (March–June 1973, and February 1974); and (3) 18 from holding tanks at the Huntsman Marine Laboratory at St. Andrews, N.B. (August 1971).

For EM, heart bloods from 18 cod at St. Andrews were Giemsa-stained, and aliquots were fixed in glutaraldehyde. Two smears showed PEN infection, and only from those 2 of the 18 cod were samples processed for EM. Delay during transport from New Brunswick to New York was less than optimal for EM, but the EICDV structure is remarkably tolerant.

For incidence and distribution data, tail-blood smears from live fish were Giemsa-stained and studied under oil immersion for 15 min before recording negatives. For the earlier records we both examined most slides to estimate percentage of red cells showing PEN. A few slides showing heavy infection were successively studied by acridine orange fluorescence in UV and by the Feulgen reaction. In each case the viroplasm was DNA-positive.

Our specimens have been supplemented by slides kindly supplied by others. In Fig. 3 we include the data of Laird and Bullock (1969). We examined their type slide of cod PEN (USNM Helminth Collection, No. 39499) and we have deposited two slides of cod PEN: No. 72592, No. 72593.

Results

Cytology

From light microscopy of infected red cells the following are the commonest signs, often present together: a basophilic cytoplasmic inclusion, with or without an attached group of granules, the virions; pycnotic or karyorrhectic nucleus; and red cell distortion.

The cytoplasmic inclusion (~0.3–1.5 μm, Fig. 1A–C) is round, compact, and Feulgen-positive. Often there is an attached group of granules, from a few to more than 50 (arrows), less basophilic than the compact inclusion. EM shows that the granules are virions and that the round inclusion is viroplasm. The viroplasm is almost always single, rarely double. When red cell membrane and nucleus are missing, whether by lysis or by damage, the viroplasm may remain attached to its coherent group of virions on the glass. Laird and Bullock (1969) showed these groups of granules, but thought that the smaller chromatin masses were the virions.

The densely staining chromatin blebs of karyorrhexis (Fig. 1B–C) may give a false impression of nuclear fragmentation, though EM shows a continuous nuclear membrane.

Red cells with large viroplasm and virion group often show more irregular outline and some cytoplasmic modification (Fig. 1C). A slide with 85% of PEN-infected red cells showed most uninfected red cells with bluer stain — immature cells not yet infected.

Ultrastructure

Electron microscopy adds information on: (a) form and structure of virions and their relation to the viroplasm; (b) assurance that even in extreme "fragmentation" of chromatin, the masses are still within a continuous nuclear membrane; (c) a frequent fibrocrystalline array of hemoglobin (Fig. 1E–F, 2B–D; not necessarily related to the PEN infection — Thomas [1971] shows such hemoglobin in normal cod blood).

Virions

The virion envelope is sharp and well stained,

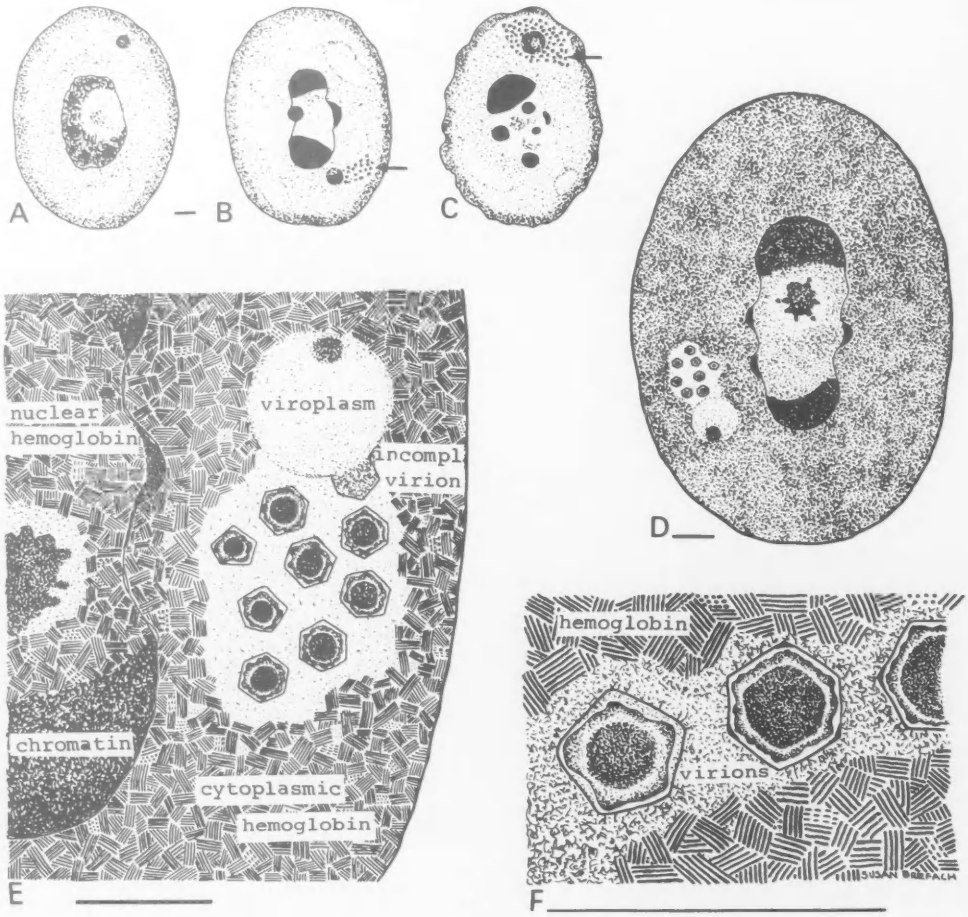

FIG. 1. Cod RBC with PEN; 3,000–50,000 ×; each line is 1 μm; A–C by light microscopy, D–F by electron microscopy; semidiagrammatic. A, nucleus with pseudovacuole; small cytoplasmic viroplasm. B, C, Chromatin condensation; cytoplasmic viroplasm with adjacent virions (arrow). D, E, Icosahedral virions in a coherent "matrix". In E one virion is forming; hemoglobin array in cytoplasm and nucleus. F, Virions show an icosahedral outer envelope (~330 nm diam), a wrinkled inner envelope, and a dense nucleoid. The pale surcoat shows vague radial pattern.

and in equatorial hexagonal section its side-to-side diameter averages 330 nm (310–350); pentagonal sections are smaller and less sharp, as tip sections of an icosahedron (Fig. 1E–F). An inner coat, thicker and less sharp, is often wrinkled (artifact?).

The nucleoid (~230 nm) is electron dense and spheroidal.

Beyond the sharp envelope is an electron lucent zone, as though a "matrix" for the virions. However, favorable sections (Fig. 2C) show that each virion has its own surcoat. Coherence of the group seems due to the mutual stickiness of these surcoats. We do not know whether this material is coded for by virus or red cell. Its texture is vaguely radial, and the outer limit is fuzzy, but center spacing of the virions is ~450 nm (350–500).

VIROPLASM

The viroplasm is generally smoothly spheroid, and finely granular–fibrillar in section. A viroplasmic condensation of unknown function is often excentrically opposite the group of virions (Fig. 1E). The virion group regularly adheres to

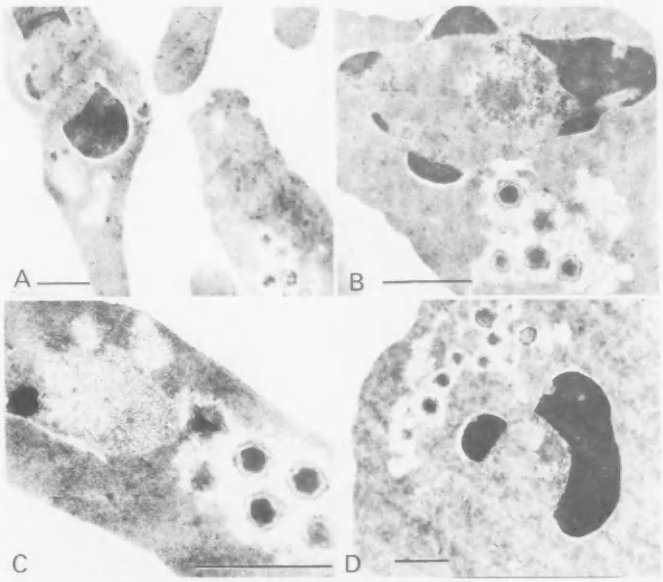

FIG. 2. Electron micrographs of sections of cod RBC with PEN. Each line is 1 μm. A, Two infected cells and tips of three normal cells. Nucleus at left shows masses of chromatin against its membrane. Pale area at left is viroplasm; at right the "matrix" of virions not in this section. Cell at right has virions in surcoats ("matrix") which separate them from each other and from the hemoglobin. B, Nucleus has condensed chromatin masses, hemoglobin, and a central sphere with radial knobs (black flecks are dirt). C, Oval viroplasm; three pale areas above are tips of viral surcoats. D, Another cell with PEN: nuclear distortion, virions, and textured hemoglobin.

the viroplasm (not always seen in random thin sections). Rarely the viroplasm includes a lamellated body with alternation of dark and medium bands separated by lighter spaces, with full repeat at ~90 nm. The pattern is unlike the lamellated bodies (membranous) shown in other EICDV infections by Stehbens and Johnston (1966) and Bernard et al. (1969); it may represent excess coat proteins.

ERYTHROCYTE NUCLEUS

EM shows not only the continuity of the nuclear membrane over the chromatin masses, but the absence of a membrane around the "pseudovacuole" from which the chromatin has moved peripherally. There is also a considerable array of hemoglobin fibrils and a spheroidal body, often with radial knobs (Fig. 1D–E, 2E). This body is not clear in Giemsa smears.

Incidence and Distribution

The present data for incidence and degree of infection are based on Giemsa-stained blood films. Figure 1, A–C, shows the normal range of appearance, though the virions are often in doubt. "Positive" cells include those with recognizable viroplasm, or with nuclear lesions characteristic of PEN. In Fig. 3 a modified symbol is used for "positive, no inclusion."

INCIDENCE

The overall incidence of PEN-infected cod (59/390, 15%) was similar to that for Georges Bank (41/256, 16%), the Boothbay Harbor, Maine, area (16/116, 14%), and New Brunswick (2/18, 11%). However, there was variation between individual samples. The October 1972 sampling on Georges Bank gave 0/48 at 13 trawl stations; the other 12 stations gave an overall incidence of 41/208 (20%). At four of these stations (positive, inclusions) there were 16/81 (20%) PEN-infected cod; 12 of the 16 infected cod showed the full pattern of nuclear lesions and viroplasmic inclusions, while the remaining 4 cod showed only nuclear lesions. At the re-

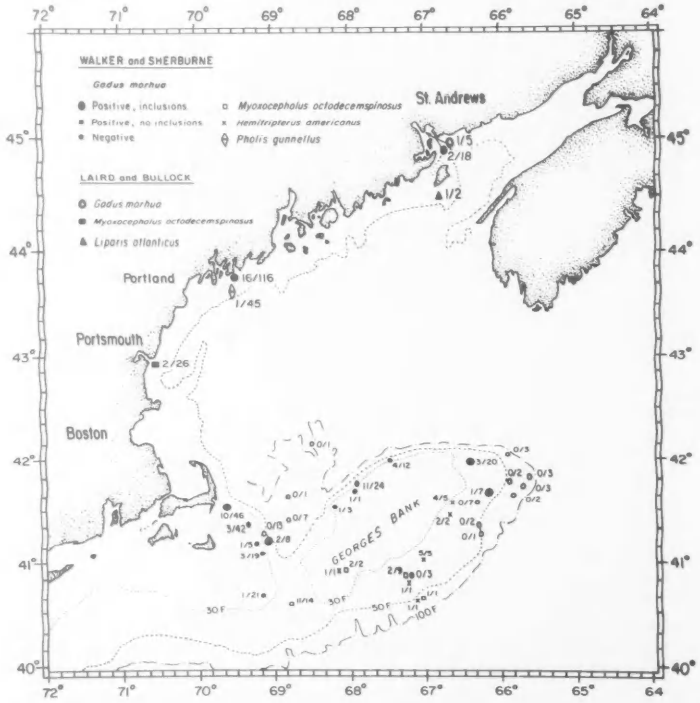

FIG. 3. Incidence and distribution of PEN for Atlantic cod, *Gadus morhua*, and four other species, from our earlier collections and those of Laird and Bullock (1969). For additional fish host species from this and other areas see text and Table 1.

maining eight stations (25/127, 20% positive) all 25 infected cod showed only the nuclear lesions; yet two of these stations showed a high incidence (4/12, 11/24). In the Georges Bank area there was higher incidence at depths of about 55 m. No PEN-infected cod from Georges Bank were taken from below 90 m, but only 38/256 were sampled at 90–185 m. Off Boothbay Harbor all cod were sampled at <90 m (5–75).

There was no significant relation of incidence of PEN to sex or total length (15–80 cm).

R. A. Khan of Memorial University, Newfoundland (personal communication) has found PEN-infected cod off Newfoundland (3/502); but none from the Grand Banks (0/11). D. A. Smail of Plymouth Polytechnic (personal communication) also reports PEN in 1/10 cod off southwest Eire.

Degree of Infection

PEN has been found only in erythrocytes, predominantly in mature ones. The heaviest infection was in a cod from Maine that had ~99% of the mature red cells infected. The full range of pattern was present, from early stages to nuclear lesions and viroplasm with virions. There was no sign of PEN in the 15% immature cells. Six other cod from the same trawl had red cell infections of <1–12%. Similarly, at the station nearest Cape Cod, the high incidence of 10/46 was matched by heavy infections: one had PEN in 85% of mature red cells; others in 60, 40, and 15%; the remaining six in 5–<1%.

Lowest degree of infection was usually in cod with nuclear lesions but not yet showing viroplasm. Two stations mentioned above, with high incidence but with only nuclear lesions, had light infections of <1–<0.01%.

PEN in Other Fish Species

We have at least 12 genera besides the cod that are affected by PEN along the Atlantic coast of North America. Laird and Bullock (1969, our Fig. 3) reported PEN in 1/2 *Liparis* from Kent Island, N.B., and in 2/26 *Myoxocephalus* from near Portsmouth, N.H. Table 1 includes these and our *Myoxocephalus*, *Hemitripterus*, and *Paralichthys* from Georges Bank, and *Pholis* from

TABLE 1. Occurrence of piscine erythrocytic necrosis (PEN) in species other than Atlantic cod, *Gadus morhua*. All data from natural populations on the Atlantic coast of North America. Our data except as noted in the footnotes.

Fish host	Location	Total no. examined	PEN incidence (%)
PEN Positive			
Alewife[a], *Alosa pseudoharengus*	Maine	718	53
Atlantic herring[b], *Clupea harengus harengus*	Maine	201	4
Rainbow smelt[a], *Osmerus mordax*	Maine	13	23
Rainbow smelt[c], *Osmerus mordax*	Maine	705	64
Rainbow smelt[c], *Osmerus mordax*	N.H.	24	63
Atlantic tomcod[c], *Microgadus tomcod*	Maine	77	35
Spot[d], *Leiostomus xanthurus*	Carolinas		
Tautog[c], *Tautoga onitis*	Long Is., N.Y.	32	3
Rock gunnel, *Pholis gunnellus*	Maine	59	5
Sea raven, *Hemitripterus americanus*	Georges Bank	15	93
Longhorn sculpin, *Myoxocephalus octodecemspinosus*	Georges Bank	26	62
Longhorn sculpin[e], *Myoxocephalus octodecemspinosus*	N.H.	26	8
Seasnail[e], *Liparis atlanticus*	Kent Is., N.B.	2	50
Fourspot flounder, *Paralichthys oblongus*	Georges Bank	4	25
Winter flounder[c], *Pseudopleuronectes americanus*	N.H.	100	12
PEN Possible[d]			
Silver hake, *Merluccius bilinearis*	N.J.		
Red hake, *Urophycis chuss*	N.J.		
Ocean pout, *Macrozoarces americanus*	Georges Bank		
Windowpane, *Scophthalmus aquosus*	N.J.		
Yellowtail flounder, *Limanda ferruginea*	Georges Bank		
PEN Negative			
Atlantic hagfish, *Myxine glutinosa*	Georges Bank	*	
Spiny dogfish, *Squalus acanthias*	Georges Bank	66	
Little skate, *Raja erinacea*	Georges Bank	*	
Alewife, *Alosa pseudoharengus*	Georges Bank	*	
Atlantic menhaden[c], *Brevoortia tyrannus*	Maine	75	
Atlantic herring, *Clupea harengus harengus*	Georges Bank	26	
Mummichog, *Fundulus heteroclitus*	Maine	287	
Fourbeard rockling, *Enchelyopus cimbrius*	Maine	*	
Haddock, *Melanogrammus aeglefinus*	Georges Bank	25	
Silver hake, *Merluccius bilinearis*	Maine	12	
Pollock, *Pollachius virens*	Georges Bank	*	
Pollock, *Pollachius virens*	Maine	98	
White hake, *Urophycis tenuis*	Georges Bank	*	
White hake, *Urophycis tenuis*	Maine	*	
Threespine stickleback, *Gasterosteus aculeatus*	Maine	*	
White perch, *Morone americana*	Maine	32	
Bluefish, *Pomatomus saltatrix*	Georges Bank	*	
Scup, *Stenotomous chrysops*	Georges Bank	10	
Cunner[c], *Tautogolabrus adspersus*	Long Is., N.Y.	25	
Atlantic mackerel, *Scomber scombrus*	Georges Bank	*	
Atlantic mackerel, *Scomber scombrus*	Maine	171	
Redfish, *Sebastes marinus*	Georges Bank	18	
Lumpfish, *Cyclopterus lumpus*	Maine	*	
Ocean pout, *Macrozoarces americanus*	Maine	*	
Ocean pout, *Macrozoarces americanus*	Georges Bank	*	
Fawn cusk-eel, *Lepophidium cervinum*	Georges Bank	*	
Butterfish, *Peprilus triacanthus*	Georges Bank	*	
Atlantic halibut, *Hippoglossus hippoglossus*	Georges Bank	*	
Windowpane, *Scophthalmus aquosus*	Maine	72	
Winter flounder, *Pseudopleuronectes americanus*	Georges Bank	*	
Goosefish, *Lophius americanus*	Georges Bank	10	

[a]Sherburne 1977; [b]Sherburne 1973; [c]Sherburne; [d]Newman personal communication; [e]Laird and Bullock 1969.

* < 10 individuals.

Maine; Sherburne's (1977) PEN-infected anadromous *Alosa* and *Osmerus* from Maine; and Sherburne's unpublished data on PEN-infected *Osmerus* from Maine and New Hampshire, *Microgadus* from Maine, *Pseudopleuronectes* from New Hampshire, and *Tautoga* from Long Island, N.Y. Although in these PEN-positive species several had quite a high incidence, the degree of infection was generally light (maximum 10% infected cells in *Hemitripterus*). The table also includes Sherburne's (1973) erythrocytic degeneration in *Clupea*, which has been confirmed as a viral infection (Philippon et al. 1977). M. W. Newman of the NMFS Laboratory in Oxford, Md. (personal communication) also reports PEN lesions with viroplasm and virions in *Leiostomus* off the Carolinas. He found other possible PEN lesions (virions not seen) in other species (middle section of Table 1). T. P. T. Evelyn of the FRB Laboratory in Nanaimo, B.C. (personal communication) has found virus in red cells of chum salmon, *Oncorhynchus keta*, and pink salmon, *O. gorbuscha* from the Pacific coast of North America.

Discussion

Morphology

Our structural findings on cod PEN are close to those of Laird and Bullock (1969) and of Appy et al. (1976), considering variations of stage, fish condition, and technique. We agree with Appy et al. that all the virions are cytoplasmic and adjacent to the viroplasm as an inclusion complex. However, their "inclusion vacuole" is shown as central in the viroplasm (their fig. 2, 6, 7). This we rarely saw with Giemsa stain; at EM level it might be either the electron-dense mass or a lamellate body. In the nucleus there is no membrane-bounded vacuole, rather a space free of hemoglobin containing a slightly denser spheroid.

Pathology

Most of our cod caught by trawling or handline gave little external indication of infection. A few were somewhat emaciated, but there were no full autopsies to check parasites or other stress factors. Sherburne (unpublished data) finds that PEN-infected cod are usually darker than noninfected in wild and captive specimens. Of the 18 tank-held cod from St. Andrews, N.B., most had some gas exophthalmia (Dehadrai 1966); of these, 16/18 were PEN-negative. R. A. Khan (personal communication) also found many cases of this "pop-eye" without PEN. Sherburne (unpublished data) has found no correlation of PEN with either "pop-eye" or external parasites in 16 cod held captive for 4 mo (November 1976–March 1977). Individual cod with natural infections, bled weekly during this time, show a slow but steady increase in degree of infection and percentage of immature red cells in the peripheral circulation. Serial bleedings are continuing. No mortalities attributed to PEN have occurred during the 4 mo. One cod from St. Andrews with heavy PEN was emaciated and moribund; it was also blind from ulcerated eyes and had so many scars and internal lesions as to cast doubt on the role of PEN. Still, we suspect that a high percentage of PEN-affected red cells, stimulating release of immature cells, must be related to physiological stress. We need further evidence, either on PEN virus as a pathogen or on the kinds of stress that may increase PEN-vulnerability. We also need evidence on methods of transmission.

Relationships

Heavy PEN infections in cod are clearly associated with a large icosahedral cytoplasmic deoxyribovirus, and so are perhaps related to Pirhemocyton, Toddia, etc., ICDV infections of other poikilotherms. When viral nature is proved or assumed, the protozoan name becomes colloquial. Not all ICDVs are surely related (Kelly and Robertson 1973); though PEN is an attractive acronym, it might be better to shift the taxonomic emphasis from fish (piscine) to blood: i.e. a group of erythrocyte ICDVs (EICDV) in which viruses have adapted to a hemoglobin environment. There will surely be taxonomic problems when there are further data on cross infectivity, pathogenicity, immunity, and biochemistry. By such criteria, even fish EICDVs in various fish host families or orders might be a relatively heterogeneous group.

Acknowledgments

This study was supported in part by grant CA 05790 from the NCI of NIH (Walker). Sherburne's work in progress, cited in text and Table 1, is supported in part by grants from NSF (PCM 75-22746) and NIH (HL 19163-01). Blood for EM (R.W. 1971) was from tank-held cod at the Huntsman Marine Laboratory, St. Andrews, N.B. At R.P.I., D. C. Gillespie and E. M. Dzaman gave technical help, and S. Brefach drew Fig. 1. Cod from Maine were obtained by Capt. M. C. McLellan, G. W. Coffin, and S.W.S. The Georges Bank samples (S.W.S.) were from a cruise (October 1972) of R.V. *Albatross IV* out of the NMFS Laboratory at Woods Hole, Mass. Other samples were obtained by

S.W.S. from local fishermen off Maine, N.H., and Montauk Pt., L.I., N.Y. G. W. Coffin of the State of Maine Fisheries Research Laboratory at West Boothbay Harbor helped with photography, and J. A. Rollins of the Bigelow Laboratory for Ocean Science prepared Fig. 3. Much work by S.W.S., G.W.C., and J.A.R. was while with the former NMFS Laboratory at West Boothbay Harbor. Contributors of PEN records are mentioned in the text. We heartily thank all those involved.

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Analysis of Zooplankton Population Fluctuations in the Strait of Georgia, British Columbia

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GARDNER, G. A. 1977. Analysis of zooplankton population fluctuations in the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 34: 1196–1206.

Canonical correlation, cluster, multiple regression, factor, and principal component analyses were used to examine zooplankton and hydrographic data over the period of unusual fluctuations in the overwintering population sizes of *Calanus plumchrus*, *C. marshallae*, and *C. pacificus* in the Strait of Georgia. Additional hydrographic data were examined for relationships between physical and biological data 3 and 6 mo out of phase. Analysis indicates a recent subtle temperature and salinity shift of uncertain biological significance. Canonical correlation and principal component analyses suggest that 15% of the variance in the zooplankton is related to a temporal trend paralleling that seen in the physical characteristics of the environment.

Based on the factor analysis, *C. plumchrus*, *Pseudocalanus minutus*, *Acartia longiremus*, *Sagitta elegans*, *Euphausia pacifica*, *Limacina* spp. and *Oithona spinirostris* are suggested as "key" species for future zooplankton monitoring programs. Statistically supported species selection can reduce the time and expense of sorting zooplankton samples without an equivalent reduction of information yield.

Key words: zooplankton, populations, *Calanus*, statistical analysis, temporal trends

GARDNER, G. A. 1977. Analysis of zooplankton population fluctuations in the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 34: 1196–1206.

Nous avons utilisé la corrélation canonique, le groupement, la régression multiple et l'analyse factorielle et par composantes principales dans l'étude du zooplancton et des données hydrographiques durant la période de fluctuations inusitées dans la taille des populations d'hiver de *Calanus plumchrus*, *C. marshallae* et *C. pacificus* du détroit de Georgie. Nous avons examiné des données hydrographiques supplémentaires en vue de détecter des relations entre les données biologiques et physiques avec décalages de 3 et de 6 mo. Cette analyse révèle un déplacement subtil récent des températures et salinités dont la signification biologique est incertaine. La corrélation canonique et les analyses par composantes principales suggèrent que 15% de la variance dans le zooplancton est liée à une tendance temporelle parallèle à celle que l'on observe dans les caractères physiques de l'environnement.

Nous basant sur l'analyse factorielle, nous suggérons *C. plumchrus*, *Pseudocalanus minutus*, *Acartia longiremus*, *Sagitta elegans*, *Euphausia pacifica*, *Limacina* spp. et *Oithona spinirostris* comme espèces «clés» dans des programmes futurs de surveillance du zooplancton. Le choix d'espèces fondé sur la statistique peut réduire le temps et les frais de triage d'échantillons de zooplancton, sans pour cela réduire le rendement en information.

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BETWEEN 1969 and 1974 unusual changes occurred in the overwintering populations of three congeneric species of planktonic marine copepod in the Strait of Georgia. One species, *Calanus plumchrus* Marukawa, is a major food source for herring, salmon, and other planktivores (Campbell 1933; LeBrasseur et al. 1969) and in the spring can produce a nearly monospecific community (Parsons et al. 1969). In November 1971 the abundance of this species appeared to be markedly less than its abundance in either December 1969 or December 1970 (J. Fulton, Pacific Biological Station, Nanaimo, personal communication). Over the same time period the numbers of *C. pacificus* Brodsky appeared to have decreased, while those of *C. marshallae* Frost had apparently increased (Gardner unpublished data). The overwintering levels of *C. plumchrus* had been stable for the 5 yr preceding the decline (Stephens et al. 1969).

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Earlier observations (e.g. Campbell 1933, 1934) are sporadic, but considered *C. plumchrus* to be the dominant local zooplankton species. Similar data do not exist for the other two *Calanus* species as they were not considered separate species in the Strait of Georgia until 1969 (Woodhouse 1971).

To examine the relationships between zooplankton species within a community and the interaction between species or species groups and the physical environment, data from a series of vertical and horizontal tows have been analyzed by a variety of statistical techniques. The results have been used to describe the extent and possible causes of fluctuations in the zooplankton community over a 5-yr period and to demonstrate an objective means of selecting "key" species and variables that can be used to minimize the amount of data that must be taken in a long-term monitoring program.

Materials and Methods

Sample Collection and Analysis

The zooplankton collections are from one of the deepest parts of the Strait of Georgia (Institute of Oceanography station *Geo 1748*) at 49°16.6'N, 123°48.4'W. In terms of zooplankton, *Geo 1748* can be considered a typical open-water Strait station (e.g. Stephens et al. 1969; Evans 1973).

Stratified tows were taken at 12 depths (10, 30, 50, 75, 100, 150, 200, 250, 300, 350, 375, and 390 m) with a modified Clarke-Bumpus opening/closing sampler (Paquette and Frolander 1957). Vertical hauls were taken from 390 m to the surface, with a 70-cm conical net. Both net types were equipped with 350-μm pore nylon mesh. All samples were preserved with neutral buffered Formalin (5% vol/vol). Although monthly samples were available, only early winter (October–December) samples were sorted. This allowed the time span covered by the analysis to be increased considerably without sacrificing an inordinate amount of time to sample sorting. In addition, in temperate regions less short-term fluctuation occurs in the zooplankton during the winter than at other times of the year (e.g. Parsons and Takahashi 1973), and thus year-to-year variation is less likely to be masked by seasonal variation.

Concurrent hydrographic data from the same depths as the stratified tows were collected by standard techniques (Institute of Oceanography 1970, 1971, 1972, 1973, 1974, 1975). As hydrographic data could not be taken on the December 1972 cruise because of time restrictions, data from November 1972 were used as the best approximation of the missing December data.

In the laboratory each vertical haul sample was placed in a tray and all large organisms removed. The sample was then split into two equal portions and one portion was further sorted. Subsampling was continued as necessary with a modified Folsom Plankton Splitter (Gardner 1972) until all species were counted. As many adults are short lived (e.g., *C. plumchrus*: Gardner 1972), adult and immediately preadult stages were sorted. Juvenile stages of major species were also counted whenever possible. For convenience, some species were sorted as groups (e.g. Williamson 1961), while in species that could not readily be separated into life-history stages, only those stages not obviously juvenile were counted.

Clarke-Bumpus samples from November and December 1971 were sorted to establish the vertical distributions of species found in the vertical hauls. In November 1971 the horizontal tows were taken between 1700 and 1800, shortly before sunset, while in December they were taken between 2400 and 0200. The vertical distribution patterns of the species were then approximated by the average position of the species in the water column. Averaging early evening and night distributions compensates for changes in distribution of the few species with diel vertical migration patterns. The data will still be slightly biased in favor of night distribution; however, the November 1971 horizontal tows are the closest to day distribution that were available for this station during the study period. For those species known to undergo diel vertical migration, the day distribution was evident in the November samples.

Using the vertical distribution patterns, the proportion of each species population in each of the three definable regions of the water column was calculated. These three regions are: near surface (0–75 m), intermediate (75–200 m), and deep (200–390 m) (Gardner 1972).

Data Treatment

Salinity and temperature values were chosen from five depths (10, 50, 200, 300, and 350 m). Stability values, expressed as $d(\text{sigma-}t)/d(\text{depth})$, were calculated over five depth ranges: 0–10, 10–50, 50–200, 200–300, and 300–350 m.

Species present in concentrations $< 0.05 \cdot m^{-3}$ and/or in $< 50\%$ of the samples were eliminated. These criteria effectively eliminate species present infrequently or in numbers too small to be estimated accurately (e.g. Marlowe and Miller 1975). The remaining species and their concentration values constitute the basic data matrix. Geary's (1936) tests for skewness and kurtosis showed nonnormality which was corrected for by a logarithmic transformation ($x' = \ln(x + 0.01)$: e.g. Williamson 1963; Cassie and Michael 1968) to produce a transformed version of the basic matrix. The concentration of each species in each month was then split into three parts based on the proportion of that species in each of the regions of the water column. This yielded the partitioned data matrix, a logarithmically transformed version of which was also produced. For some analyses, particularly those involving expensive computer time and requiring more consistent data, it was an advantage to further reduce the number of species being considered. In these cases, species that had

barely met the criteria for inclusion in the basic zooplankton matrix were also eliminated, yielding the core species matrix.

Statistical Procedures

Unless otherwise noted, the analyses were performed via library programs available on the IBM 370/168 system at the University of British Columbia. The library reference name is given when each program is first mentioned. Where applicable, the 10% probability level was used for rejection of the null hypothesis. Since the intent of my analysis is not so much rigorous as it is heuristic, using a slightly lower than normal criterion for significance minimizes the possibility of discarding a biologically meaningful result of borderline statistical significance. To isolate such results, I have divided tests that show $P \leqslant 0.10$ into three ranges of significance: $0.01 \geqslant P$, $0.01 < P \leqslant 0.05$, $0.05 < P \leqslant 0.10$.

The partitioned data matrix was initially clustered by species and months using a cluster analysis program maintained by R. Foreman, Department of Botany, University of British Columbia. The matrix of concentration values was double standardized and converted to a matrix of percent similarity values by a minimum distance function. Clusters were then formed using an agglomerative technique based on maximum similarity, with clustered groups averaged to produce "new" clusters in successive iterations.

To examine phase relationships between hydrographic and biological data, canonical correlations (UBC BMD 06M) were calculated between biological and physical data blocks in phase and 3 and 6 mo out of phase. Hydrographic data for these comparisons were obtained either from Institute of Oceanography data reports (1970–75) or from original data. For the canonical correlations, the species in the transformed core species matrix were first grouped according to their position in the water column (Table 1). *Calanus plumchrus* and *C. marshallae* were run as single species "groups" in addition to being run within their own groupings. Significance levels for the canonical correlations were calculated from the lambda statistic using Bartlett's test (Cooley and Lohnes 1971).

The core species were then regressed individually (using UBC *STRP) against each hydrographic variable in the same phase relationships as for the canonical correlations. The subdivisions of each hydrographic variable were treated as a series of five independent variables against which the dependent variable, ln (0.01 + no. of species "A"/m^3), was regressed. Regression with more than one hydrographic variable at a time was avoided in this first approach due to the difficulty of interpreting apparent interactions between the three variables. Only significant (F prob $\leqslant 0.10$) variables were included in the final regression equation.

Factor analysis (UBC *FAN) of the partitioned, transformed basic data was then carried out, the largest grouping generated being refactored to increase the resolution of the factors. Finally, principal component analyses (UBC BMD 01M) of the winter hydrographic data and the core species biological data were carried out to gain further information on the degree of redundancy in the data, the most influential components of the community, and the internal structuring of the data banks.

TABLE 1. Grouping of species by vertical distribution pattern, for use in the canonical correlation analysis.

Group/characteristic	Species
1. Min concn at intermediate depths, some vertical migration	*Euphausia pacifica* *Nanomia bijuga* *Pareuchaeta elongata* (< CIV and total) *Sagitta elegans*
2. Min concn in deep water, but > 10% of the population in each region of the water column	*Euprimno abyssalis* *Parathemisto pacifica*
3. Min concn near surface, most species with a mid-depth max; at least 10% of the population in each region of the water column	*Tomopteris septentrionalis* *Metrida pacifica* (< CIV) *Chiridius gracilis* Ostracods
4. All species with a max concn in deep water, and a negligible concn (< 10% of the total) in near-surface water	a) *Calanus plumchrus* *Pseudocalanus minutus* *M. pacifica* (≥ CIV) *C. marshallae* *C. pacificus* b) *C. plumchrus*[a] c) *C. marshallae*[a]

[a]These species were run as separate "groups" in addition to being included in the main group.

Results and Discussion

Hydrographic Regime During the Study Period

The distribution of hydrographic parameters conforms with previously published descriptions of the hydrography of the Strait of Georgia (Tully and Dodimead 1957; Waldichuk 1957; Gardner 1972; Evans 1973). The annual cycle is typified by the fluctuations in 1971–72 (Fig. 1). In spring the upper part of the water column is strongly stratified due to the warming of surface water by insolation and the lowering of near-surface salinity by runoff. Waters deeper than 200 m are cool and have low (<31‰) salinity with little temperature or salinity gradient.

In late summer, salinity in deep water has increased to 31.15‰ and temperatures are all close to 9.0°C due to an intrusion of warmer, more saline water formed by mixing processes in the southern approaches to the Strait of Georgia. There is no noticeable change in the stratification

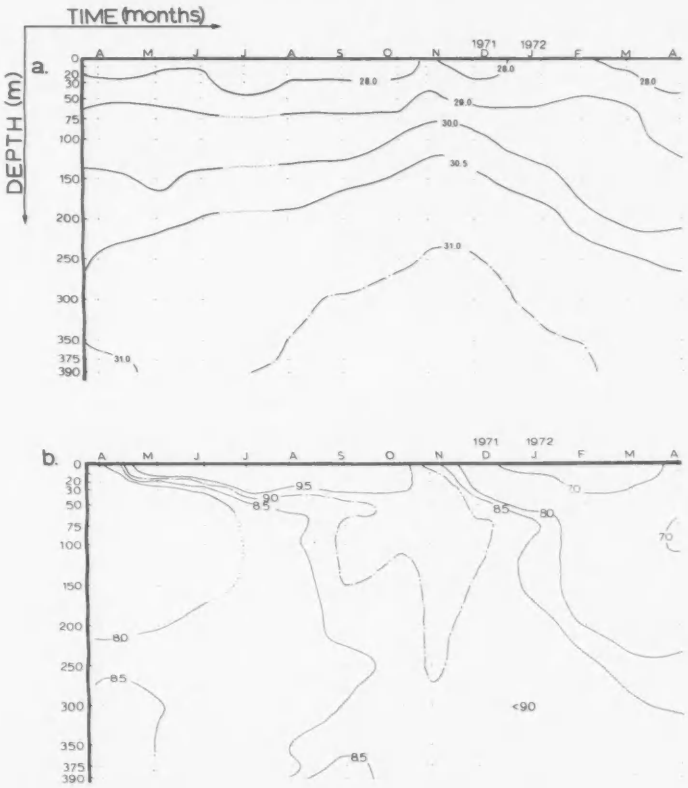

FIG. 1. Hydrographic variation at *Geo 1748* between April 1971 and April 1972. a, Salinity isopleths in parts per thousand. b, Temperature isopleths in degrees Celsius. Dotted lines indicate interpolations over missing data points, dashed lines the 31‰ and 9.0°C isopleths for a and b, respectively. Sampling depths are indicated by a small dot.

of water deeper than 50 m; however, near-surface stability is beginning to decrease. By November intrusions have further increased the temperature and salinity of *Geo 1748* deep water. Water of greater than 31‰ is now found at 250 m compared to 300 m in November. Salinities and temperatures below 50 m are generally higher in winter than at any other time of the year. Stability is still low and has also decreased between the surface and 50 m; the density gradient in December is <0.01 over all depth ranges examined.

To put these data into perspective, they must be compared with the other years for which data are available. With one exception, the data show a gradual increase in the salinity of the intruding water mass throughout the study period (Fig. 2). Pickard (1975), examining the same phenomenon over a shorter time period, felt that while it indicated a trend towards higher deep water salinities, such changes were quite small. The changes are more apparent when 1974 salinities are added to Pickard's data.

Similar but more tenuous trends can be described for temperature. Temperatures above 9.0°C at depths >50 m have been less common since 1970–71, with the 9.0°C isotherm only reaching the deepest depths sampled in 1973–74. The absolute changes are small; deep-water temperatures of >9.5°C or <8.75°C were rarely noted. These trends are also supported by the statistical analysis of hydrographic data. The most obvious feature of the analysis is the previously established division of the water column into three regions (Gardner 1972); however, the temporal trend shows up in the case ranking on the first principal components of temperature and salinity (Table 2).

TABLE 2. Rank order of standardized cases on each principal component of the hydrographic parameters. Case codes: 1 — Oct. 1969; 2 — Nov. 1969; 3 — Dec. 1969; 4 — Nov. 1970; 5 — Dec. 1970; 6 — Nov. 1971; 7 — Dec. 1971; 8 — Dec. 1972; 9 — Nov. 1973; 10 — Dec. 1973; 11 — Dec. 1974.

	Temperature			Salinity			Stability			
Rank	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	4th
1	8	5	6	2	2	6	4	8	7	4
2	7	11	10	1	11	10	6	7	2	5
3	11	7	4	3	9	4	7	6	6	2
4	6	10	7	7	4	2	5	9	4	8
5	10	3	3	6	10	7	9	3	9	10
6	1	9	9	8	5	3	10	1	1	7
7	9	8	5	5	7	8	8	2	5	1
8	3	2	11	9	1	11	3	11	3	9
9	2	4	2	4	3	1	11	4	11	6
10	5	1	8	10	8	9	1	5	8	3
11	4	6	1	11	6	5	2	10	10	11

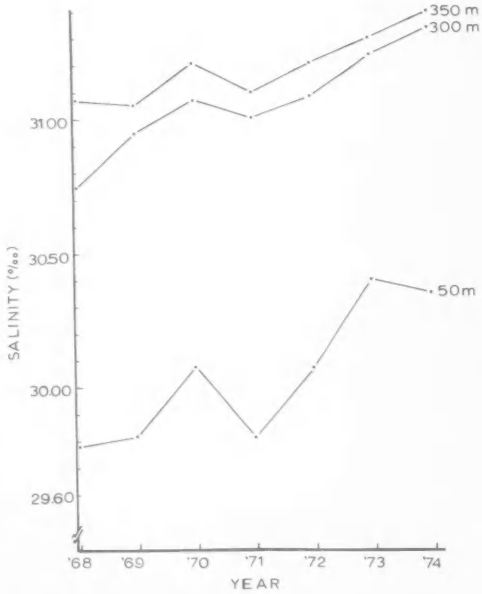

FIG. 2. Fluctuations in salinity at selected depths in successive Decembers at *Geo 1748*. (Data for 1972 are from November.)

Changes between years can result from fluctuations in the incoming Juan de Fuca water or in the degree of mixing of this water with outgoing fresher water. In the former case, changes in the characteristics of Juan de Fuca water might reflect fluctuations in the intensity of offshore upwelling or in the degradation of upwelled water as it moves in through Juan de Fuca. In either case, properties of the mixing water masses other than temperature and salinity (e.g. content of organic carbon, trace metals, particulates, nutrients, etc.) can also vary and lead to variation in the "quality" of the intruding water. These changes in water quality may be associated with, and perhaps responsible for, concomitant changes within the zooplankton community.

ZOOPLANKTON DATA

Over 75 taxa were identified and counted. The bulk of these taxa were single species that are either associated with cold temperate waters or are widespread, but at least two of the copepods, *Gaidius columbiae* and *Bradyidius saanichi*, are endemic to the Strait of Georgia (Park 1966, 1967). Two other copepods, *C. pacificus* and *Aetideus armatus*, are warm transitional water species (Brodsky 1950; Woodhouse 1971). Reduction of the original data block left 29 taxa, divided into 32 subdivisions, which form the basic data matrix (Table 3). The core species matrix consists of the 20 subdivisions marked in Table 3 (14 species, 1 group, and 2 subdivided species).

RELATIONSHIPS WITHIN THE COMMUNITY

The most obvious feature of the zooplankton community is its separation into groups of species with common vertical distribution patterns. This separation is not sufficiently well defined to suggest the presence of three separate communities; however, it can account for much of the variance in the zooplankton data. For example, a group of deep-water species dominates one of the two main species clusters formed in the cluster analysis (Fig. 3). These same deep-water species all have high loadings on the first factor of the zooplankton data factor analysis, a factor which is associated with 34% of the zooplankton variance (Table 4). Although other vertical distribution

TABLE 3. Proportion of each species in each of the regions of the water column found at *Geo 1748*. Acronyms are included to facilitate later reference to the species in figures. *Core species.

Species	Acronym	Region		
		Near surface (0–75 m)	Intermediate (75–200 m)	Deep (200–390 m)
**Cyphocaris challengeri*	CYPHOC	0.14	0.17	0.69
**Euprimno abyssalis*	EUPRIM	0.56	0.28	0.16
**Parathemisto pacifica*	PMISTO	0.27	0.51	0.22
Scina borealis	SCINA	0.03	0.17	0.81
**Sagitta elegans*	SAGELE	0.23	0.10	0.67
Aegina sp.	AEGINA	0.57	0.43	—
Aequorea sp.	AEQUOR	—	0.30	0.70
*Medusa sp. A	MEDSPA	0.07	0.35	0.58
Muggia atlantica	MUGGIA	0.29	0.54	0.17
**Nanomia bijuga*	NANOM	0.32	0.18	0.50
Acartia longiremus	ACARLO	0.95	0.05	—
**Calanus marshallae*	CMARSH	—	0.07	0.93
**C. pacificus*	CPACI	0.01	0.16	0.83
**C. plumchrus*	CPLUM	—	—	1.00
Candacia columbiae	CANDAC	0.13	0.10	0.77
**Chiridius gracilis*	CHIRID	0.27	0.42	0.31
**Eucalanus bungii bungii*	EUCAL	0.01	0.02	0.97
Gaidius columbiae	GAIDCO	0.16	0.46	0.38
Metridia okhotensis	METOK	—	0.03	0.97
**M. pacifica* (≥CIV)	MPAC1	0.02	0.04	0.94
(<CIV)	MPAC2	0.21	0.40	0.39
Oithona spinirostris	OSPIN	0.10	0.57	0.33
**Pseudocalanus minutus*	PSEUDO	—	0.02	0.98
**Pareuchaeta elongata* (<CIV)	PAR1	0.44	0.15	0.41
(≥CIV)	PAR2	0.27	0.41	0.32
(total)	PARTOT	0.35	0.24	0.40
**Euphausia pacifica*	EUPAC	0.71	0.02	0.28
**Tomopteris septentrionalis*	TOMSEP	0.10	0.45	0.45
Clione limacina	CLLIM	0.19	0.50	0.31
Limacina helicina	LIMAC	0.06	0.39	0.55
Larvaceae (*Oikopleura* sp.)	OIKOP	0.46	0.13	0.41
*Ostracods	OSTRAC	0.20	0.31	0.49

patterns can be identified in the data, the deep-water species constitute the most consistent and largest group.

Factor analysis also suggests that there is a high degree of redundancy in the collected zooplankton data. The initial factor analysis produced eight factors, significant by the Guttman criterion (discarding eigenvalues <1.0: Guttman 1954), which together yield 90% of the variance in the zooplankton data matrix. The factors are most closely related to species with common vertical distribution patterns, as discussed above. Refactoring the group of 13 species associated with the first factor produced seven factors incorporating virtually 100% of the variance. After varimax rotation, the individual contributions of the factors to the variance were more equitable. The factors were again related to vertical distribution patterns, but with greater resolution than in the initial factoring.

The redundancy indicated by the ability of a small number of factors to reproduce most of the variance in a matrix of 32 variables results from a lack of any a priori basis for selecting "key" species on which to concentrate a monitoring program. This problem is unfortunate in view of the expense involved in collecting oceanographic data and of the time required to sort zooplankton samples. Similar considerations of expense and time have often led to zooplankton monitoring programs that are not species specific but yield data such as "wet weight biomass of total zooplankton," "total copepods," "zooplankton displacement volume," or similar measures of abundance (e.g. Stephens et al. 1969). When individual species are monitored, the species are often chosen subjectively rather than objectively. There can be considerable merit to these approaches, depending on the purposes for which the data are collected; however, it is dangerous

TABLE 4. Summary of factor analysis of zooplankton.

Factor	% of variance associated with factor (after varimax rotation)	Species with factor loadings >0.7 absolute value (*negative loadings)
Initial factoring		
1	34	CPLUM, PSEUDO, MPACI, EUCAL, METOK, CMARSH, SCINA, MUGGIA*, AEGINA*, ACARLO*
2	16	PARTOT*, EUPAC*, PAR1*, SAGELE*, OIKOP*
3	13	PMISTO*, LIMAC*
4	10	TOMSEP*, OSPIN*, GAIDCO*
5	7	MPAC2
6	7	PAR2
Refactoring of factor 1[a]		
1	27	CPACI, SCINA, CMARSH
2	21	ACARLO*, AEGINA*
3	13	CYPHOC*
4	12	MUGGIA
5	8	CANDAC*

[a]Species in this list, but not listed under factor 1 above, had low (<0.7) loadings in the initial factoring.

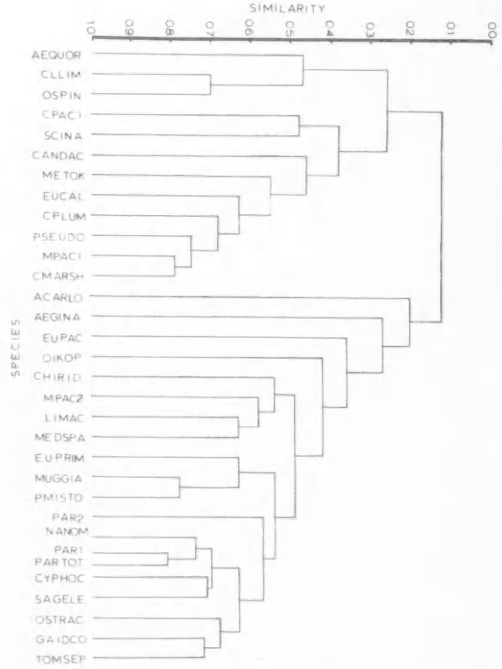

FIG. 3. Clustering of species based on partitioned raw data.

to lump species haphazardly. Factor analysis provides an objective criterion for selecting key species when it is neither logistically nor economically feasible to monitor all species.

Using the information generated by factor analysis of my zooplankton data, and the vertical distribution patterns indicated from the sample sorting and other statistical analyses, a small group of species can be selected that are representative of the general community. Such a group might contain *C. plumchrus*, *Pseudocalanus minutus*, *Acartia longiremus*, *Sagitta elegans*, *Euphausia pacifica*, *Limacina* spp. and *Oithona spinirostris*. These seven species, which are all readily identified, are the major representatives in factors accounting for 75% of the variance in the zooplankton community. Use of only these species would considerably reduce sample sorting time without an equivalent reduction in information gain. If data from this block of species indicated greater than usual variation in the species or an apparent trend in the population interactions, then it might be advisable to sort and count samples more thoroughly. Otherwise, the amount of work involved in monitoring the zooplankton community would be greatly decreased.

A distinct temporal bias can also be identified within the zooplankton data. Clustering of the partitioned data with months as variables yields three clusters distinct at the 0.50 level on a

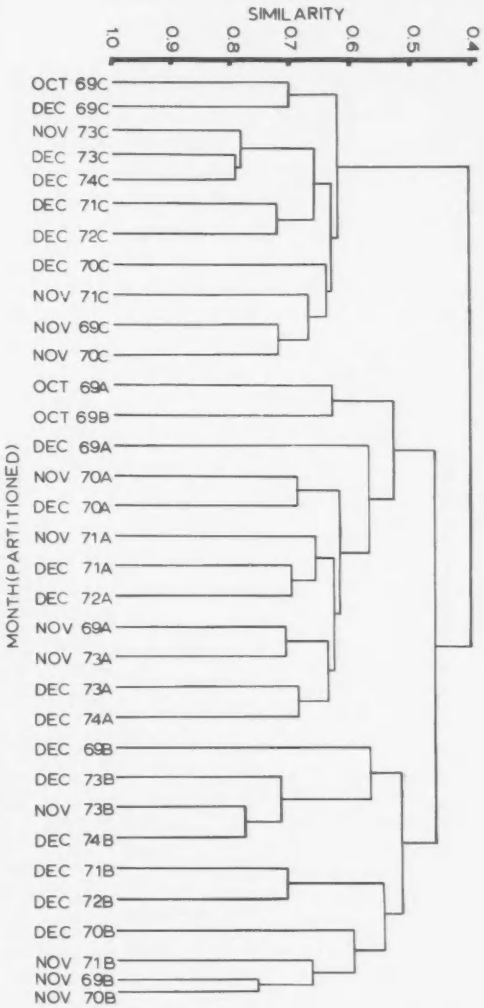

FIG. 4. Clustering of samples. A = near surface, B = intermediate, C = deep water.)

similarity scale from 0.0 to 1.0 (Fig. 4). Each cluster consists of data from one of the three regions of the water column found at the station. The only exception is the inclusion of intermediate-water data from October 1969 within the cluster of near-surface water. In the clusters of deep- and intermediate-water data, there is a tendency for November data to be grouped separately from December data and for data taken in the latter part of the sampling period to be grouped separately from earlier data.

This tendency is also seen in the ranking of standardized cases on the principal components of the zooplankton (Table 5). The rankings on the first two components are related to deep- and intermediate-water samples, respectively, reiterating the importance of vertical distribution patterns. The ranks of the standardized cases on component three, however, are temporally arrayed. The third principal component of the zooplankton is not associated with any single species or species group, suggesting that the temporal trend is a function of the community rather than of any small group of species. Furthermore, the third principal component is associated with 15% of the zooplankton variance. Subsequent rankings also tend to be more closely associated with the time sequence of the samples than with specific groups of organisms. The temporal trend within the zooplankton data parallels that in the hydrographic data and suggests strong links between the physical and biological regimes.

RELATIONSHIPS BETWEEN THE ZOOPLANKTON AND ENVIRONMENTAL PARAMETERS

The significant canonical correlation coefficients, all at least 0.90, more clearly define the relationship between hydrographic parameters, particularly temperature and stability, and zooplankton data (Table 6). Significant correlations are found for all of the phase relationships with time, but overwintering stocks of zooplankton appear to be particularly influenced by conditions in the preceding August and September.

The character of the relationship between hydrographic and biological data is further defined by the regression analysis. The majority of the significant regression equations involve only a constant and one independent variable of the five tested simultaneously, and also show the relationship of zooplankton with temperature and stability indicated by the canonical analysis. Although temperature and stability are related, only two species show simultaneous significant regressions on both parameters. This suggests that the effects of temperature and stability regimes on zooplankton species are, in at least some cases, independent.

It is not surprising that the hydrographic regime in late summer affects the size of overwintering zooplankton stocks; however, the relationship appears to be as important as, or perhaps more important than, the effects of the hydrographic regime during the preceding spring phytoplankton bloom when reproduction was at a peak. Two basic processes contribute directly or indirectly

TABLE 5. Rank order of standardized cases on each principal component of the zooplankton. Case codes: see Table 2; depth codes: a — 0–75 m, b — 75–200 m, c — 200–390 m.

Zooplankton components	Rank																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1st	3c	10c	9c	7c	1c	8c	11c	5c	2c	4c	3b	6c	10b	9b	7b	1b	8b
2nd	1b	10b	11b	3b	5b	9b	2b	8b	7b	4b	6b	1a	1c	10a	10c	11a	3a
3rd	7a	7b	7c	8a	8b	10a	8c	10b	10c	11a	11b	11c	9a	9b	9c	5a	6a
4th	3a	3b	3c	10a	4a	10b	10c	9a	5a	4b	11a	4c	7a	9c	9b	1a	5c
5th	7b	7c	7a	4b	3b	8b	4a	4c	3a	3c	8a	8c	5b	2b	1b	2c	6b
6th	6b	6c	6a	3b	3c	3a	9b	11b	7b	4b	2b	9a	9c	11a	11c	10b	7c
7th	8c	8a	8b	11c	11b	10a	11a	10c	2a	3a	2c	10b	2b	3b	3c	4a	4b

	Rank															
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1st	11b	5b	2b	4b	6b	3a	10a	9a	7a	1a	11a	8a	5a	4a	2a	6a
2nd	5a	11c	2a	9a	3c	5c	2c	9c	8a	8c	7a	7c	4a	6a	4c	6c
3rd	5b	5c	6b	6c	1a	1b	1c	3a	3b	3c	4a	4b	4c	2a	2b	2c
4th	11c	5b	11b	7c	7b	1b	1c	6a	8a	2a	6c	6b	8b	8c	2c	2b
5th	1c	5c	2a	5a	1a	6c	6a	11b	9b	11a	10b	11c	9c	9a	10c	10a
6th	7a	8b	4a	2c	2a	4c	10c	10a	8c	1b	8a	1a	1c	5b	5a	5c
7th	4c	5a	5b	5c	1a	7a	6a	1c	7c	6c	7b	6b	1b	9a	9c	9b

TABLE 6. Summary of the significant canonical correlation coefficients. Figures indicate percent of zooplankton variance associated with the appropriate hydrographic factor. T = temperature; S = salinity; St = stability. *Significant at $p \leq 0.10$; **significant at $p \leq 0.05$; ***significant at $p \leq 0.01$; (significance based on chi-square probability). Group numbers refer to the groups listed in Table 1. Paired figures indicate significant correlations with the first and second canonical factors of the hydrographic parameter.

	Data in phase			Data 3 mo Out of Phase			Data 6 mo Out of Phase		
Group	T	S	St	T	S	St	T	S	St
1	23**	—	26**	21*	24*	27**	8*	15**	—
2	—	—	—	11**	—	—	12.3*** 80.9**	—	—
3	—	—	30**	—	—	52**	13**	28**	—
4a	26***	—	23**	—	25*	13*	—	34**	30** 10*
4b	77*	—	—	—	—	98***	—	—	—
4c	80*	—	—	88*	—	—	98***	—	—

to the effect of late summer/early fall hydrographic data on overwintering zooplankton stocks. These processes are the availability of phytoplankton and the characteristics of the deep-water intrusion that is forming at this time and moving up the Strait.

Although many factors can affect phytoplankton production, an increase in production in fall will be partially regulated by the availability of nutrients and by the presence of sufficient light for net phytoplankton production. Nutrient renewal will be related to the degree of water column stability that must be overcome for physical-mixing processes to effectively introduce deep-water nutrients into near-surface waters. High surface stability in late summer and early fall, in conjunction with decreasing day length at this time of year, can consequently reduce the biomass of phytoplankton available for grazing. This reduction would be detrimental to herbivores still building up stores of lipids in preparation for overwintering (e.g. Lee et al. 1970a, b). Reduced overwintering success in herbivores would in turn affect other trophic levels and could conceivably result in reduced production levels throughout the Strait of Georgia.

The composition of the intruding water mass also affects overwintering zooplankton and provides a mechanism by which near-surface hydrographic characteristics can affect deep-water

species. Some possible mechanisms for generating fluctuations in the composition of this water were described earlier and include variations in outgoing near-surface runoff water and incoming deep Juan de Fuca water. In addition, the degree of mixing will vary with water column stability, mixing energy, and the relative proportions of each type of water. The quantity of runoff water is an important component in this variation and will also strongly affect near-surface hydrographic characteristics.

Because of the inherent variability in the components of this system, the "quality" of deep water for the growth and survival of zooplankton can be expected to vary from year to year. There is no a priori basis for these variations to have a long-term temporal component. As previously discussed, however, principal component analysis demonstrates a temporal bias to the fluctuations in the hydrographic regime, while principal component and cluster analyses show a similar temporal trend within the zooplankton. Based on my results, and on other papers that indicate the effect of water "quality" on the survival of copepods (e.g. Lewis et al. 1971, 1972), the subtle changes in the zooplankton community are probably due to variations in the hydrographic characteristics of the environment.

Changes in temperature, salinity, or stability per se may not be the causal factor in the zooplankton changes. They do, however, indicate changes in the general hydrographic regime and thus are related to changes in a myriad of factors, such as dissolved and particulate organic carbon, nutrients, trace metals and the like.

One particularly intriguing aspect of the regression analysis concerns the relationship between *C. plumchrus* and *C. marshallae*. The regression of the two species against temperature at 350 m, a depth at which the populations overlap considerably (Woodhouse 1971; Gardner 1972), yields regression lines of opposite slope that intersect in the region of normal ambient temperature (Fig. 5). As discussed above, this should not necessarily be construed as a temperature effect. It is equally likely the result of changes in unknown water quality parameters associated with the changes in temperature.

The relationship between the two species is further complicated by the fact that, although they are very similar species, *C. plumchrus* can effectively filter particles of a smaller size than *C. marshallae* and most other copepods can handle (Gardner unpublished data). This may give *C. plumchrus* a selective advantage over *C. marshallae* which modifies the apparent "temperature" effect currently favoring *C. marshallae*.

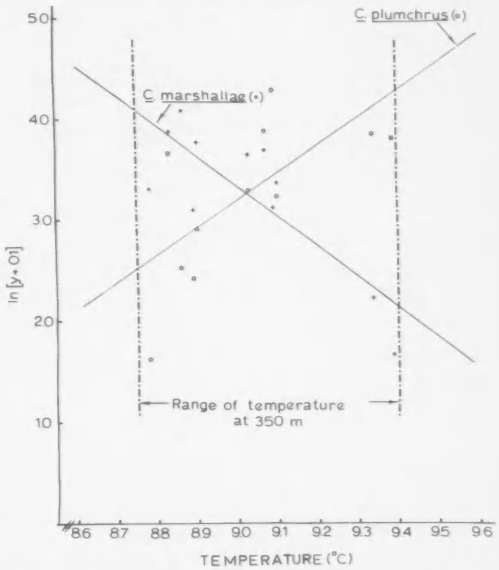

FIG. 5. Regressions of *Calanus plumchrus* and *C. marshallae* against temperature at 350 m. Equations of the form: $\ln(y + 0.01) = mx + b$.

The association of deep-water temperatures with population levels of these two important copepod species, and the demonstration of parallel long-term temporal trends in the hydrographic and biological regimes, suggest that the Strait of Georgia is in a state of flux. Whether this is a transient shift that will eventually change directions or part of a longer term trend that may accelerate in future cannot be resolved with the data currently available. The former possibility may be more probable; however, monitoring designed to uncover long-term trends should continue. Such studies may be very important to future management and conservation programs for the Strait of Georgia and will greatly improve our understanding of the complex interactions between the physical and biological components of the system.

Acknowledgments

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Intertidal Kelp Response to Seasonal Environmental Changes in a British Columbia Inlet

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DRUEHL, L. D., AND S. I. C. HSIAO. 1977. Intertidal kelp response to seasonal environmental changes in a British Columbia inlet. J. Fish. Res. Board Can. 34: 1207–1211.

Sporophyte response of three kelp species, *Laminaria saccharina* (L.) Lamouroux, *Alaria tenuifolia* Setchell, *Costaria costata* (Turner) Saunders, in the intertidal zone of Burrard Inlet was correlated primarily with tidal and atmospheric conditions and not with salinity or nutrients. Young sporophytes first became evident in February and March when insolation was increasing and the lower low tides were shifting from night to day. These sporophytes were distributed from 1.3 m above 0 tide to below 0 tide. By April all plants above 0.7 m had died and the remaining plants achieved their maximum biomass in May. The subsequent decrease in biomass was related to prolonged daytime exposures to air. *Costaria costata* produced meiospores by July before dying and *L. saccharina* and *A. tenuifolia* persisted until autumn when they produced meiospores.

Key words: kelp, Laminariales, phenology, environment, growth

DRUEHL, L. D., AND S. I. C. HSIAO. 1977. Intertidal kelp response to seasonal environmental changes in a British Columbia inlet. J. Fish. Res. Board Can. 34: 1207–1211.

La réponse des saprophytes de trois espèces de varechs (*Laminaria saccharina* (L.) Lamouroux, *Alaria tenuifolia* Setchell, *Costaria costata* (Turner) Saunders, dans la zone intertidale de l'inlet Burrard est liée avant tout aux conditions atmosphériques et de marée, et non à la salinité ou aux éléments nutritifs. Les jeunes saprophytes apparaissent en février et mars, alors que l'insolation augmente et que les basses marées de vive-eau passent de nuit à jour. Ces saprophytes sont répartis entre 1.3 m au-dessus du niveau 0 à au-dessous du niveau 0 de la marée. En avril, toutes les plantes situées au-dessus de 0.7 m étaient mortes, et les autres atteignirent leur biomasse maximale en mai. La diminution subséquente de la biomasse est liée à des expositions prolongées à l'air pendant le jour. *Costaria costata* produit de méïospores en juillet avant de mourir, et *L. saccharina* et *A. tenuifolia* vivent jusqu'en automne, alors qu'ils produisent des méïospores.

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DUE to the potential economic value of kelp (Phaeophyta, Laminariales) it is important to understand the response of these plants to their environment (Hasegawa 1976). Earlier studies in British Columbia have correlated seaweed distributions with various oceanographic parameters (e.g. Druehl 1967; Scagel 1961, 1963; Widdowson 1965), or have followed chemical changes in kelp over time (Whyte and Englar 1974, 1975a–c; Wort 1955). To our knowledge there have been no published accounts that have considered kelp response to seasonal variation of the oceanographic environment in British Columbia. Druehl (1967) related the distribution of two kelp to seasonal seawater temperatures and salinities but he did not take into account nutrients or atmospheric features.

The purpose of this study was to examine seasonal changes in selected environmental parameters occurring at two sites in Burrard Inlet, and to relate these to the growth and reproduction of three intertidal kelp species: *Laminaria saccharina* (L.) Lamouroux, *Alaria tenuifolia* Setchell, and *Costaria costata* (Turner) Saunders.

Materials and Methods

Nutrients (NO_3, NO_2, PO_4, I), salinity, and air and seawater temperatures were monitored weekly at two sites in Burrard Inlet from July 1968 to June 1971. Sampling was conducted on the ebbing tide within an hour of the lower low tide.

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Seawater subsamples were scooped with a plastic beaker along 20 m of shore. The final samples were a composite of approximately 20 subsamples. Seawater temperature and salinity (Goldberg Refractometer, American Optical Co.) were determined immediately. The sample was then filtered through glass wool, frozen with dry ice, and returned to the laboratory for chemical analysis. Colorimetric chemical analyses were performed with a Hitachi Perkin-Elmer model 139 UV-Vis spectrophotometer using the following methods: nitrate (Wood et al. 1967), nitrite (Bendschneider and Robinson 1952), phosphate (Strickland and Parsons 1968), and total inorganic iodine (Dubravčić 1955). Duplicate determinations were made for all measurements.

Insolation data were for the University of British Columbia, Vancouver (Anon. 1968–71a). Tide and current data were from published accounts (Anon. 1962; Anon. 1968–71b). Air temperatures were measured in the shade near high water level at the time of seawater sampling.

Phenological observations were made at least fortnightly over the 3-yr study period. Kelp fresh weights were determined at irregular intervals between March and May 1969 and March and June 1970. Thirty of the largest plants observed were collected from the 0.3–0.0-m tide level. These were placed in plastic bags, sealed, and returned to the laboratory where they were gently blotted and weighed. Fresh weights of the 20 largest plants were recorded. Care was taken to collect these plants from different, but adjacent regions throughout the study period.

The study sites (Brockton Point and Lumberman's Arch) were located on the northeast side of Stanley Park, Vancouver (Fig. 1). The studied beaches had a 1:7–1:15 slope and the substrate was mud with bivalve shells and scattered rock. A sewage outfall located between the two sites delivered untreated sewage and storm drainage during the period of this study. The average rate of delivery was 0.26 m^3/s and the maximum rate was 0.60 m^3/s (Greater Vancouver Sewerage and Drainage District personal communication).

Results and Discussion

Tides, Currents, and Atmospheric Conditions

The study area was subjected to mixed semidiurnal tides, having a maximum amplitude of 4.9 m (Anon. 1968–71b). The studied kelp were exposed to atmospheric conditions during periods of low spring tides at night November through February and during daylight hours April through August. During March, September, and October the kelp were not exposed during the low tides (Fig. 2). The greatest number of exposures to air by the kelp occurred during June–July and December–January (11–13 exposures per month) when the duration of the single longest exposure was greatest (4–4.5 h, Fig. 2).

Ebbing tides near the study sites had velocities

FIG. 1. Location of the study sites, Lumberman's Arch and Brockton Point, and the sewage outfall, with current patterns and velocities.

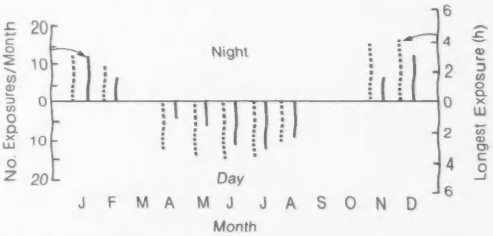

FIG. 2. Number of exposures per month, duration of the longest exposure for each month, and the distribution of these two tidal features between day and night. These data are applicable for 0.7 m above 0 tide level.

2–6 km/h and during flooding tides, 2–8 km/h (Anon. 1962). Due to a prominent back-eddy generated during flood tide, nearshore water movement was always from Brockton Point to Lumberman's Arch (Fig. 1).

The air temperatures reported here were taken within an hour of the lower low tide which occurred during the day in the spring and summer and at night in autumn and winter. Air temperatures were similar for the two study sites (Fig. 3). The mean monthly maxima (18–18.3°C) occurred during July–August and the mean monthly minima occurred during December–February (−2 to 6°C).

Minimum insolation values occurred in December (43–51 ly/day) and maximum values occurred in June–July (525–574 ly/day, Fig. 3, Anon. 1968–1971).

Seawater Temperature, Salinity, and Nutrients

As observed at low tide, seawater temperatures and salinities varied inversely over the 3-yr period (Fig. 4). Maximum temperatures of 15–16°C occurred in July and minimum temperatures of 4.5–7°C occurred in January. Maximum salinities

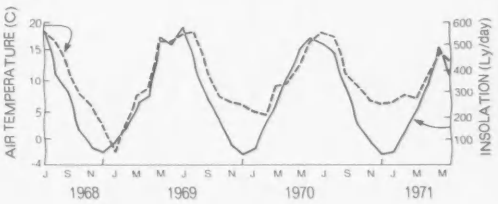

FIG. 3. Monthly mean air temperatures and insolation values for the study period. Temperatures are averaged for the two study sites.

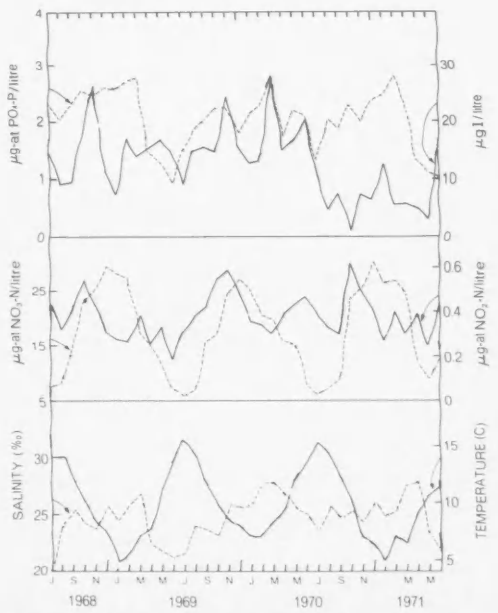

FIG. 4. Monthly mean nutrient levels, salinities, and seawater temperatures for Brockton Point. The solid lines relate to the right-hand scales and the broken lines relate to the left-hand scales.

(26.7–28‰) occurred in February, March, and April and minimum salinities (20–23.5‰) occurred in June and July. Temperatures and salinities for the two stations were similar.

Of the four nutrients monitored, nitrate showed the most pronounced seasonal cycling (Fig. 4). Nitrite and phosphate concentrations, while demonstrating some seasonality, were irregular. Inorganic iodine did not show any seasonal cycling. Maximum levels of nitrate (25.5–27.3 µg-at NO_3-N/ℓ) occurred in June–August. Maximum (0.47–0.65 µg-at NO_2-N/ℓ) and minimum (0.14–0.32 µg-at NO_2-N/ℓ) nitrite concentrations occurred just prior to the maximum and minimum nitrate levels. Maximum phosphate levels (3.9 µg-at PO_4-P/ℓ) generally occurred between January and March and minimum levels (1 µg-at PO_4-P/ℓ) occurred during the summer months. Total inoragnic iodine varied irregularly throughout the study period, with concentrations ranging from 1 to 30 µg I/ℓ.

Nutrient levels were somewhat higher at Lumberman's Arch than at Brockton Point. The 3-yr averages for Lumberman's Arch were 18.14 µg-at NO_3-N/ℓ, 0.42 µg-at NO_2-N/ℓ, 2.32 µg-at PO_4-P/ℓ, and 14.82 µg I/ℓ; and at Brockton Point they were 17.83 µg-at NO_3-N/ℓ, 0.38 µg-at NO_2-N/ℓ, 2.07 µg-at PO_4-P/ℓ, and 12.89 µg I/ℓ.

KELP PHENOLOGY

The three kelp species studied are potential perennials. However, intertidally, the vast majority of plants behaved as annuals. No differences in phenology were noted between the two stations.

Sporophytes, identifiable as those of the studied species (i.e. 3–5 cm long), first became evident during February and March. During this period low temperature and relatively high salinity and nutrient conditions prevailed. Further, this was a transitional period between night low tides and day low tides. Thus, while insolation values were relatively low, the amount of light being filtered by the water column was less.

Microscopic sporophytes of *L. saccharina* are known to be produced at Lumberman's Arch throughout the year, but subsequent development into macroscopic forms occurs only from February to March (Hsiao and Druehl 1973c). Thus, the appearance of macroscopic forms is determined by environmental action on the microscopic sporophyte and not the preceding gametophyte generation. *Laminaria saccharina* from our study sites are euryhaline and eurythermal (Druehl 1967). Further, the production of sporophytes is not affected by nutrients (PO_4, NO_3, I) in the concentrations observed over the 3 yr at our study sites (Hsiao and Druehl 1973a, b). Of the considered parameters, insolation appears to be critical. We hypothesize that total solar energy received per time determines the time of macroscopic sporophyte appearance. The increasing illumination at a time of low temperature would result in a high photosynthesis to respiration ratio, beneficial to growth. Studies by Kain (1964), Hsiao and Druehl (1971), and Vadas (1968) indicate that total daily solar energy received, rather than daylength or intensity alone, is the important light function in early kelp development.

Maximum biomass for *C. costata* occurred in

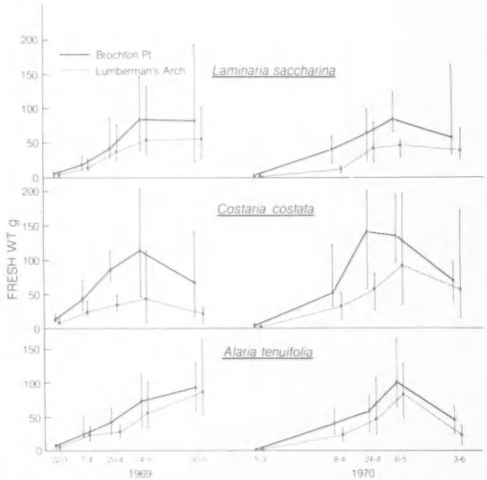

FIG. 5. The mean and range of wet weights for the 20 largest individuals observed for each species.

early May 1969 for both populations and in early May 1970 for the Lumberman's Arch plants and April–May 1970 for the Brockton Point plants (Fig. 5). The maximum biomass was not determined for the other two species during 1969. In 1970 the maximum biomass was recorded for these species in May.

During the period of biomass decrease, distal portions of the blades were discolored. Initially, green areas were observed over the brown blade. On subsequent low tides these green areas had turned white and finally the damaged tissue was lost. We rarely observed this phenomenon on the meristematic region of the blades. A similar damage pattern was observed on plants covered with ice during winter exposures to air.

Change in kelp biomass is the result of two processes. First, the addition of new tissue which occurs in the meristematic region at the blade base, and second the loss of older tissue through erosion occurring at the distal end of the blade (Mann 1973). Druehl (1965) has shown that growth continues during the period of biomass decrease for *L. saccharina* at Lumberman's Arch, but at a slower rate than earlier in the year. We believe that the exposure to atmospheric conditions initiates a more rapid erosion rate and is primarily responsible for the decrease in biomass, and that the decreased growth rate is a contributing factor.

Laminaria saccharina remained vegetative until September when some of the population initiated sorus development. By October all observed *L. saccharina* had sori and by January most of these plants were gone. Those plants that persisted through the winter initiated vegetative growth in February and produced sori from April to June and again in October. *Alaria tenuifolia* followed the same temporal pattern as *L. saccharina*. However, *A. tenuifolia* initiated sporophyll development in April and these continued to develop until sori were produced beginning in September. Many of the *A. tenuifolia* plants bore sori on the blades as well as on the sporophylls. *Costaria costata* remained vegetative until April when sori were produced. By late July, the total intertidal population of *C. costata* had died off.

The meristematic regions of all three kelp species demonstrated a greater tolerance to meteorological conditions during air exposure than did the adjacent vegetative tissue. This permitted intertidal representatives of *A. tenuifolia* and *L. saccharina* to survive exposure during the daylight low spring tides and persist until autumn when they produced reproductive tissue. The inability of *C. costata* to persist through the summer may reflect a slower growth rate relative to the erosion rate of vegetative tissue. Schmitz and Lobban (1976) have shown that photosynthate produced by the blades of British Columbia kelp is translocated to the meristematic region. This indicates that the loss of the older tissue would directly affect the growth potential of the meristem. Lüning (1970) has demonstrated that the meristem of *L. hyperborea* is dependent on the older vegetative tissues. Thus, the three kelp species assured themselves intertidal space by either releasing their meiospores during the period of great environmental stress (*C. costata*) or by persisting through this period and releasing their meiospores in the autumn (*L. saccharina*, *A. tenuifolia*).

VERTICAL DISTRIBUTIONS

In late winter young sporophytes of the three species, attached to stable substrate, were more or less uniformly distributed from below zero tide to 1.3 m above zero tide. A few plants were observed higher in the intertidal zone, attached to shell fragments and small pebbles. Possibly these had been moved shoreward through water motion. By late March–mid April all plants higher than 0.7 m above zero tide had died except for those occupying tide pools. This dieback related to the increased exposure to atmospheric conditions. The even distribution of the young sporophytes, above the 0.7-m tide level, suggests they arose from a blanket recruitment of meiospores originating from the deeper plants. Gametophytes

arising from these meiospores are able to develop and persist during periods environmentally hostile to the macroscopic sporophytes. In the case of *C. costata* this period extends through the summer to late winter; for *L. saccharina* and *A. tenuifolia* it extends through late winter. The distribution of functional gametophytes to 1.3 m above 0 tide level allows these species the opportunity to repeatedly challenge, through new genotypes, a physiologically hostile environment.

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Response of the Crayfish *Orconectes virilis* to Exploitation

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MOMOT, W. T., AND H. GOWING. 1977. Response of the crayfish *Orconectes virilis* to exploitation. J. Fish. Res. Board Can. 34: 1212–1219.

Life tables can aid in assessing the impact of exploitation of the crayfish *Orconectes virilis* by fish, invertebrates, and man. The major response of the population to exploitation comes through an adjustment of both the m_x column (egg production) and l_x (survivorship). Fish and invertebrate predation were directed towards modification of the early portion of the l_x column. Survivorship did not change appreciably.

Exploitation by man was directed toward males rather than females. An indirect result was an increase in the l_x values for females. However, this was counteracted by a decrease in m_x values leading to population stability as indicated by the R_0 values. Both the exploitive strategies of fish and man failed to extract the maximum available biomass from the production of a given year-class.

Key words: crayfish, exploitation, *Orconectes virilis*, life tables

MOMOT, W. T., AND H. GOWING. 1977. Response of the crayfish *Orconectes virilis* to exploitation. J. Fish. Res. Board Can. 34: 1212–1219.

Les tables de mortalité peuvent aider à évaluer les effets de l'exploitation de l'écrevisse *Orconectes virilis* par les poissons, les invertébrés et l'homme. La principale réponse de la population à l'exploitation se fait par un ajustement à la fois de la colonne m_x (production d'œufs) et de la colonne l_x (aptitude à survivre). La prédation par les poissons et les invertébrés fut orientée vers une modification de la portion du début de la colonne l_x. La survie ne changea pas de façon appréciable.

L'exploitation par l'homme a été orientée vers les mâles plutôt que les femelles. Un résultat indirect a été l'augmentation des valeurs de l_x pour les femelles. Cependant, ceci a été compensé par une diminution des valeurs de m_x, ce qui conduisit à la stabilité de la population, comme l'indiquent les valeurs de R_0. Les stratégies d'exploitation tant par les poissons que par l'homme ne réussirent pas à extraire la biomasse disponible maximale produit par une classe d'âge donnée.

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THE crayfish *Orconectes virilis* is a key component of the intermediate level of production in aquatic ecosystems because of its polytrophic role and biomass dominance (Flint and Goldman 1975). Fish predation is a common source of stress on crayfish populations. Numerous reports document the importance of crayfish in the diet of fish, e.g. Reid (1972) and Snow (1971). However, they do not measure the impact of fish on the crayfish, nor the response by the crayfish to this predation. Although a few studies, notably Svardson (1972), Ricketts (1975), and Taub (1972), claim that fish can eradicate crayfish populations, none of them directly measured changes in the population dynamics of the crayfish in response to fish predation. Ricketts (1975) cited Taub as evidence that fish can eradicate crayfish populations but Taub's (1972) study suffers from sampling deficiency. Only Svardson's comments on the importance of the eel, *Anguilla anguilla*, as a crayfish predator seems substantiated in nature. The impact of predation of trout on crayfish populations in the Pigeon River Forest lakes of Michigan is given in Gowing and Momot (1974). These crayfish populations were subject to predation by fish, invertebrates, and man. This paper shows how life tables can be used to assess the effects of exploitation on crayfish populations and thus help improve our insights into the

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TABLE 1. Estimates of the age composition of the total female population in West Lost and North Twin lakes from 1966 to 1973.

	No. at hatching				
	0.0	0.5	1.5	2.5	3.5
		West Lost			
1966	172,887	30,187	2,137	1,313	34
1967	130,280	28,412	2,545	2,178	12
1968	92,468	12,436	2,109	1,245	159
1969	117,482	21,171	2,746	1,893	145
1970	74,261	20,498	2,893	1,613	39
1971	81,153	25,274	5,107	1,287	17
1972	53,434	10,938	2,144	1,042	25
1973	43,068	16,408	1,203	872	
		North Twin			
1966	55,794	24,085	2,410	984	84
1967	88,345	20,152	3,442	1,425	27
1968	130,057	12,718	2,450	934	124
1969	66,993	26,759	1,440	1,242	175
1970	36,628	27,043	3,039	1,430	99
1971	58,873	10,726	3,835	991	110
1972	51,429	5,943	3,607	1,122	11
1973	33,464	5,895	1,218	435	

reasons for their frequent biomass dominance in aquatic communities. In addition, life tables provide a quantitative measure of the stress imposed by various types of predation on the population.

Study Area and Methods

The two study lakes, North Twin and West Lost, are located in the Pigeon River State Forest in the north central portion of the lower Peninsula of Michigan, about 86 km south of the Straits of Mackinac. They are of similar geologic origin, size, morphometry, and water chemistry and, as designated research waters, public fishing is excluded. The study was conducted from May 1966 to September 1973.

Crayfish were collected with baited wire traps and nets. In each lake traps were deployed in a radial pattern as illustrated in Momot and Gowing (1972) so that the lake was sampled to a depth of 10 m. These samples are well below the hypolimnion and extend to the depth at which oxygen becomes limiting to crayfish (Momot and Gowing 1972).

Age composition was analyzed from size-frequency polygons verified by following the modal progression of groups of previously marked animals of known age (Momot 1967a) as well as using arithmetic probability-paper as described by Hopkins (1967). Length of carapace was measured to nearest 0.5 mm with vernier calipers. Growth rate and age were determined from a series of size-frequency graphs plotted at intervals during the growth season.

Seasonal growth in weight was determined by converting length to weight using a length–weight regression computed from empirical data obtained from trap catches and netting of the young. Instantaneous rates of natural mortality, after sequential population estimates, and instantaneous growth rates, were used to estimate production (Ricker 1958). Migration is not possible in these lakes since they have neither an inlet nor outlet and therefore it can be eliminated as a source of change in the proportions of different year-classes and as having any effect on mortality rate calculations.

Fecundity and the size of an initial cohort were determined from average counts of eggs attached to the pleopods of females. Recruitment was determined by population estimates made in the autumn of the young-of-the-year crayfish hatched in the spring.

Life tables were constructed from age-composition data on the populations (Table 1) and estimates of the mean number of attached eggs per female (Table 2). Age composition of the female population (Table 1) was used to construct the l_x column in the life table (Table 3). The age composition was determined from mark and recapture estimates made in the spring and summer. The population estimates were then subdivided into age-groups by construction of size-frequency polygons mentioned above. The m_x column in the life tables was constructed by taking the mean number of attached eggs (Table 2) and assuming a 50:50 sex ratio to give the number of female eggs per female of each age per year (Table 3). Ricker's production model was suitable for crayfish since both growth and mortality closely approximated exponential functions.

No fishery existed prior to the study and we created a fishery subject to prior knowledge of crayfish population dynamics and regulations applied in a commercial fishery in Wisconsin. During 1970, 30 baited traps were fished 5 consecutive days during the last

TABLE 2. Egg production of *Orconectes virilis* in two lakes. Data presented as mean number of attached eggs ± SE (*n*).

	Age-group	$\bar{x}$ ± SE (*n*)
	North Twin	
1967	II	61.0±4.6 (47)
	III	103.9±17.9 (7)
1968	II	100.8±7.0 (21)
	III	144.9±8.8 (12)
1969	II	64.2±7.4 (35)
	III	135.6±35.7 (5)
1970	II	44.5±6.1 (40)
	III	76.0±21.2 (6)
1971	II	51.9±7.5 (28)
	III	72.4±22.4 (5)
1972	II	42.8±5.5 (45)
	III	113.8±19.5 (8)
1973	II	31.7±4.2 (39)
	III	110.0±26.0 (2)
1974	II	22.8±2.8 (43)
	III	38.5±4.2 (5)
1975	II	82.4±4.2 (15)
	III	91.1±19.5 (15)
	West Lost	
1967	II	48.8±4.7 (30)
	III	99.9±8.6 (12)
1968	II	80.7±5.8 (29)
	III	115.9±7.6 (14)
1969	II	73.6±5.3 (42)
	III	98.6±17.8 (10)
1970	II	51.3±6.5 (27)
	III	83.9±10.6 (21)
1971	II	36.9±5.2 (47)
	III	49.1±11.3 (15)
1972	II	53.5±10.5 (43)
	III	96.8±17.7 (8)
1973	II	41.5±5.2 (39)
	III	124.0±25.1 (2)
1974	II	17.7±2.9 (27)
	III	56.5±5.4 (10)
1975	II	41.5±6.2 (22)
	III	78.1±10.6 (11)

week in August for a total of 150 trap days in each lake. All crayfish less than 30 mm carapace length were returned to the lake and those 30 mm or larger were removed. The size limit of 30 mm carapace length protected the female brood stock because most females bred once before reaching this length and were correspondingly older than males of the same size. Age 2 and 3 males were harvested from the population. The maximum yield harvest removes the largest weight on a sustained basis. After the initial harvest, application for the Paulik–Bayliff equilibrium yield model indicated that maximum yield harvest was achieved in West Lost Lake but the population in North Twin was underharvested. The model prescribed a doubling of effort of at least 300 trap days for North Twin. Therefore, during the last 2 yr of this study (1972–73), we used 60 traps (in North Twin) for a 5-day interval. The trapping period was always confined to the last 2 wk of August throughout the study.

TABLE 3. Life tables for female crayfish from North Twin and West Lost. $R_o = \Sigma l_x m_x$, represents the net increase per generation, l_x = probability of survival out of 1000 recruits at start, m_x = number of eggs per female per year.

	Age (yr)	l_x	m_x	$l_x m_x$
		North Twin		
1966–67	0.0	1.000		
	0.5	0.431		
	1.5	0.042	30.50	1.28100
				0.83120
	2.5	0.016	51.95	R_o = 2.11220
1967–68	0.0	1.000		
	0.5	0.228		
	1.5	0.039	50.40	1.96560
				1.15936
	2.5	0.016	72.46	R_o = 3.12496
1968–69	0.0	1.000		
	0.5	0.097		
	1.5	0.018	32.09	0.57762
				0.40680
	2.5	0.006	67.80	R_o = 0.98442
1969–70	0.0	1.000		
	0.5	0.396		
	1.5	0.015	22.26	0.33390
				0.45600
	2.5	0.012	38.00	R_o = 0.78990
1970–71	0.0	1.000		
	0.5	0.738		
	1.5	0.080	25.98	2.07840
				1.30320
	2.5	0.036	36.20	R_o = 3.38160
1971–72	0.0	1.000		
	0.5	0.181		
	1.5	0.063	21.42	1.34946
				0.85305
	2.5	0.015	56.87	R_o = 2.20251
1972–73	0.0	1.000		
	0.5	0.115		
	1.5	0.070	15.86	1.11020
				0.11000
	2.5	0.002	55.00	R_o = 1.22020
		West Lost		
		l_x	m_x	$l_x m_x$
1966–67	0.0	1.000		
	0.5	0.174		
	1.5	0.012	24.38	0.29256
				0.34965
	2.5	0.007	49.95	R_o = 0.64221
1967–68	0.0	1.000		
	0.5	0.218		
	1.5	0.019	40.36	0.76684
				0.98549
	2.5	0.017	57.97	R_o = 1.75233
1968–69	0.0	1.000		
	0.5	0.133		
	1.5	0.021	36.81	0.77301
				0.59160
	2.5	0.012	49.30	R_o = 1.36461

TABLE 3. (*Concluded*)

	Age (yr)	l_x	m_x	$l_x m_x$
1969–70	0.0	1.000		
	0.5	0.175		
	1.5	0.022	25.64	0.56408
				0.62895
	2.5	0.015	41.93	$R_o = 1.19303$
1970–71	0.0	1.000		
	0.5	0.276		
	1.5	0.038	18.46	0.70148
				0.51513
	2.5	0.021	24.53	$R_o = 1.21661$
1971–72	0.0	1.000		
	0.5	0.311		
	1.5	0.063	26.76	1.68588
				0.77392
	2.5	0.016	48.37	$R_o = 2.45980$
1972–73	0.0	1.000		
	0.5	0.204		
	1.5	0.040	20.73	0.82920
				1.17800
	2.5	0.019	62.00	$R_o = 2.00720$

Results

The life table results can be analyzed to interpret the response of crayfish populations to an experimental fishery and to natural predation. Changes in survivorship for any age-group with time are reflected in the l_x column; changes in egg production are reflected in the m_x column. These two forces, survivorship and egg production, determine the ability of the population to resist any external stress on the population. The net result is reflected in R_o which represents the net increase or decrease in the population per generation. Over the course of many generations R_o should remain near 1.0, provided the population is adjusting to the many stresses placed upon it. An additional advantage of analysis by the life table method is that the relative contribution of each age-class to R_o (net increase per generation) can be easily assessed.

We first wish to interpret the response of the population to the experimental trap fishery. Because of the selectivity of the traps during the fishing season (late August), the fishery selected mostly males rather than females from the population. The reasons for trap selectivity are discussed in Momot and Gowing (1972). Over the course of time the selective harvest of males resulted in a proportional increase in the female population. The increased survival of females as the result of the removal of adult males is reflected in the higher l_x values of age 1.5 females in both West Lost and North Twin Lake. The mean $l_x \pm$ SD value for the preexploitation period (1966–70) was 0.028 ± 0.014 compared to a mean $l_x \pm$ SD value of 0.070 ± 0.008 for the exploitation period (1970–73). This is more than a twofold increase (statistically significant at the 0.01 level, $t = 4.602$).

TABLE 4. Turnover ratio (P:$\overline{B}$) and yield ratio (P:Y) for young-of-the-year crayfish during their first two growing seasons while being cropped by brook trout and rainbow trout. P = production, $\overline{B}$ = mean biomass, Y = yield to trout (consumption). P, $\overline{B}$, and Y measurements in kilograms. (Data derived in part from Gowing and Momot 1974.) (BT) = brook trout, (RBT) = rainbow trout, (–) = no trout stocked or present.

	P	B	Y	P:B	P:Y
1966 West Lost (BT) June 66–Aug. 67	131.2	27.2	56.5	4.8	2.3
1966 North Twin (BT) June 66–Aug. 67	129.2	27.5	0.8	4.1	153.8
1966 South Twin (BT) June 66–Aug. 67	131.1	29.9	1.6	4.4	81.4
1968 West Lost (BT) June 68–Aug. 69	82.7	20.5	13.4	4.1	6.2
1968 North Twin (RBT) June 68–Aug. 69	81.9	21.2	9.1	3.9	9.0
1969 South Twin (–) June 68–Aug. 69	122.8	21.6	–	5.7	–

In West Lost Lake the mean $l_x \pm$ SD value for the preexploitation period (1966–70) was 0.018 ± 0.004 compared to a mean $l_x \pm$ SD value of 0.047 ± 0.014 during exploitation (1970–73), a significant twofold increase ($t = 3.946$, at the 0.01 level). This by itself should have led to a large increase in the population since survival rate of the brood stock was increasing over time as exploitation began. However, during the same intervals lower m_x values occurred in both lakes. In North Twin Lake the mean number of female eggs per female adult ± SD from 1966 to 1970 was 33.81 ± 11.86. During the exploitation period (1970–73) it was one third lower with a mean value of 21.08 ($t = 1.711$, $0.10 > P > 0.05$). In West Lost the mean m_x values ± SD from 1966 to 1970 was 31.79 ± 7.98 while the mean m_x values during 1970–73 were 31% lower at 21.98 ± 4.29 ($t = 1.902$, $0.10 > P > 0.05$). Even though both these differences were significant at only the 0.10 level, the large t values were very close to the 0.05 level of significance and we feel certain that a larger sample size would have produced a significant difference.

The lower values during exploitation are of strategic importance to the population dynamics of this species since it is the 1.5 age-group that constitutes most of the reproductive potential of the population. *Orconectes virilis* breeds at age 2 and again at age 3. Even though the breeding

population consists of age 2 and 3 females, only small numbers of females reach age 3 to breed a second time (Table 1). In most years the breeding success of the population depends mainly on the survival and subsequent fecundity of the 1.5 females. Age 2.5 females may be thought of as an important strategic reserve and occasionally contribute a large fraction of the overall production of young. However, in certain years, especially when R_o was low as in 1968–69 and 1969–70 in North Twin Lake, a substantial fraction of R_o was due to the reproductive effort of Age 3 females (Table 3). This was also true in West Lost during 1966–67, 1969–70, and 1972–73.

The corresponding decrease in the m_x values as the l_x values increased helped maintain population stability. This is reflected in the R_o values which represent the net increase per generation and are the summation over all age intervals of the l_x and m_x columns (Table 3). Though the values fluctuate from year to year there is no overall trend evident for the exploitation period compared to the preexploitation period (Table 3). Hence, the population could be said to be adjusting to the additional stress imposed by exploitation through the fishery. The interaction between male specific mortality, population density, and egg production served to maintain numerical stability and is evidence for a self-regulating mechanism in the population.

Discussion

Life table statistics can also be applied to the analysis of the crayfishes response to other predators as well. Trout in our lakes prey on crayfish until the crayfish reach an age of 1.5 yr. For the crayfish population in our study, at normal fish predator densities, the trout had little impact in controlling final population size or production (Gowing and Momot 1974). Only the low l_x value of 0.174 for age 0–0.5 in West Lost Lake during 1966–67 may have been caused by fish predation (Table 3). The fish population density in West Lost (at that time 1399/ha) was nearly 10 times that of North Twin Lake (Momot and Gowing 1974). The latter lake had a density of only 188 fish/ha and a corresponding l_x value of 0.431 for this same age-group of crayfish (Table 3).

Fish predation may have contributed to the low l_x value of 0.097 for age 0.5 in North Twin during 1968–69. Yet during more intensive predation within the same time period in West Lost, the l_x value was 0.133 (Table 3). Low values for l_x of age 0.5 crayfish were also recorded in 1971–72 in North Twin and West Lost in 1969–70 with no fish present in the lake.

The negligible effect of fish predation is further illustrated by the R_o values for the crayfish populations during the year when fish were present compared to the years when fish were absent. The values in North Twin were 0.98–3.12 from 1966 to 1969 (years when fish were present) compared to 0.79–3.38 in the absence of fish. In West Lost R_o values were 0.64–1.75 in the presence of fish and 1.19–2.46 in the absence of fish. The 0.64 value was recorded at a fish density far above normal for the lake. Remarkably the range of R_o values over the years when fish were present compared to years when they were absent were substantially the same. Hence in most cases fish do utilize crayfish as a forage but rarely have the devastating impact on them reported for cladocerans and other microcrustaceans.

Dragonfly predation was another source of mortality that operated early in the life span of a cohort. In general, West Lost showed a much higher recruitment per square metre for young-of-the-year crayfish than North Twin. Dye and Jones (1975) have shown that the abundance of Aeschnid dragonflies was much higher in North Twin and that they were a large potential source of mortality for newly hatched, 6–12-mm crayfish in both lakes. However, the rate of mortality between young-of-the-year from West Lost and North Twin was not different and the higher recruitment was attributed to more available nursery area and a larger female breeding population in West Lost Lake. Greater food availability may be responsible for the larger female adult population. Hence during the age interval 0.0–0.5 dragonflies share young-of-the-year crayfish with trout. However, insect predation, like that of fish, proved compensatory for other factors operating in the environment. This is simply because both fish and dragonflies fed on the youngest age-group; thus, mortality from fish and insect predation was compensatory for other factors operating in the environment. Predation is just one of many sources of mortality that give crayfish steep survivorship curves — or stated alternatively, fish and dragonflies eat crayfish that would die anyway.

Predator efficiency between fish and trap fishery can be compared with regard to utilization of the annual production of the crayfish biomass. Although production of crayfish during their first two growing seasons was similar in all three lakes and fish predation was concentrated on these age-classes, predation failed to exceed 15% of crayfish production in most years (Table 4). Despite rather uniform turnover ratios ($P:\bar{B}$) in both lakes, only in West Lost from June 1966 to

August 1967 was there an appreciable harvest of the available production, 56.5 kg out of a production of 131.2 kg for a yield ratio of 2.32. At lower fish densities yield ratios were high. Since crayfish production was similar in both lakes the fish in West Lost were more efficient predators than those in the other lake. Whether this marked difference in predator efficiency was due to higher densities of the fish population or an inherent feature of West Lost Lake cannot be resolved. Stocking larger fish (267 nm mean length) at equal densities (430/ha) in North Twin and West Lost did not result in better utilization of crayfish. Brook trout were stocked again in West Lost and rainbow trout in North Twin (Gowing and Momot 1974). Fish were not stocked in a control lake, South Twin. Despite similar though lower production in both North Twin (81.93 kg) and West Lost (82.66 kg), the brook trout in West Lost once again obtained higher yields (13.44 kg) than rainbows in North Twin (9.11 kg) (Table 4). At the same time production of crayfish in South Twin was similar to that in 1966. Turnover ratios ($P:\bar{B}$) during 1968 were similar in both lakes and comparable to the earlier period. Brook trout make better use of crayfish than rainbow trout since they forage more on benthos (Alexander and Shetter 1969). The P:Y ratio shows that predator efficiency declined from approximately 40–45% in 1966 to about 15% in 1968 with increase in the size of the brook trout. However, the numbers of fish stocked also declined. Probably this had a greater effect than the change in size on predator efficiency. Nevertheless, the fish densities in 1966 in West Lost and 1968 in West Lost and North Twin were far above the average of 250 fish/ha normally stocked. At these average densities brook trout utilized only about 5% of the production (Momot 1967b).

We can contrast the yields from the experimental trap fishery with those from fish predators. The fishery harvested mainly age 1, 2, and 3 male crayfish compared to the harvest of only age 0 crayfish by the trout. The fishery was especially effective in removing age 2 crayfish as indicated by the lower yield ratios (Table 5). Note the P:Y in the trap fishery for age 2 crayfish is far below that of trout on age 0 crayfish, indicating good utilization. For age 1 crayfish, yield ratios to the trap fishery are much higher, indicating poor use of this age-group. The lowest yield ratio (P:Y) for age 1 crayfish was 5.37 for North Twin in 1972. Most were much higher, ranging from 8.83 to 40.53.

For trout the turnover ratios for age 0 crayfish were quite high, 3.85–5.68 (Gowing and Momot 1974), while for age 2 crayfish, the target of the trap fishery, turnover ratios were 0.22–2.55 (Table 5).

Gulland (1970) suggested that in a well-managed fishery the catch should be, at best, half the total production including the production of fish smaller than the sizes being caught. The brook trout in West Lost in 1966 approached this goal in harvesting crayfish.

If we consider all three age-groups the trap fishery did not approach a harvest efficiency of 50%. The trap fishery was fairly efficient in harvesting age 2 and 3 crayfish as indicated by the yield ratio for age 2 and 3 crayfish (Table 5).

Considering the population production of crayfish rather than that of specific age-groups, neither the trout nor the trap fishery allowed the population to accumulate its maximum biomass before harvesting a crop. Watt (1968) gives two alternate strategies for the harvest of a particular prey. If population size is governed by intrinsic factors, one should allow production to reach its maximum value before harvesting the prey. But where

TABLE 5. Annual turnover ratios ($P:\bar{B}$) and yield ratios (P:Y) for male crayfish being cropped by the experimental fishery. P = annual production, B = mean biomass, Y = yield to the fishery, P. $\bar{B}$, and Y measurements in kilograms.

Lake	Year	Age-group	P	$\bar{B}$	Y	$(P:\bar{B})$	(P:Y)
WL	1970	I	47.1	19.4	5.1	2.4	9.2
		II	13.6	29.3	29.1	0.2	0.2
		III	0.3	0.7	0.7	0.4	0.4
NT	1970	I	21.1	14.9	0.5	1.4	40.5
		II	11.6	17.5	9.5	1.2	0.7
		III	0.1	0.8	0.4	0.5	0.2
WL	1971	I	24.4	13.0	2.4	1.9	10.4
		II	9.6	24.5	12.4	2.6	0.8
		III	3.3	0.7	0.4	4.7	8.5
NT	1971	I	28.4	13.9	1.4	2.0	20.5
		II	8.7	13.9	7.8	0.6	1.1
		III	2.4	0.6	0.6	4.3	3.9
WL	1972	I	25.0	10.2	1.4	2.5	17.5
		II	7.5	16.8	10.4	0.4	0.7
		III	3.3	1.9	2.1	1.8	1.6
NT	1972	I	18.9	9.7	3.5	2.0	5.4
		II	10.9	16.3	11.9	0.7	0.9
		III	2.7	0.8	0.3	3.3	9.9
WL	1973	I	25.4	11.4	2.9	2.2	8.8
		II	8.7	15.4	8.9	0.6	1.0
		III	3.4	2.2	0.6	1.6	6.1
NT	1973	I	15.2	10.3	0.9	1.5	17.5
		II	6.0	17.3	7.2	0.4	0.8
		III	2.6	2.0	1.4	2.6	1.9

TABLE 6. Annual production of crayfish in kilograms per lake by age-group. (Data from 1966 to 1969 taken in part from Gowing and Momot 1974.)

West Lost	1966–67	1967–68	1968–69	1969–70	1970–71	1971–72	1972–73
Sex ♂							
Age-group							
0	28.6	14.5	33.2	16.1	9.6	18.8	12.5
1	37.0	37.3	32.1	47.1	24.4	25.0	25.4
2	29.6	9.9	15.4	13.6	9.6	7.5	8.7
3	14.9	5.9	3.0	0.3	3.3	3.3	3.4
Total	110.1	67.6	83.7	77.1	46.9	54.6	50.0
Sex ♀							
0	32.0	14.9	22.2	17.9	8.8	16.7	12.6
1	32.7	30.4	18.9	25.7	27.6	40.0	15.7
2	11.0	5.7	6.4	3.0	1.8	4.6	4.5
3	1.6	3.3	1.7	1.5	0.7	2.1	1.4
Total	77.3	54.3	49.2	48.1	38.9	63.4	34.2

North Twin	1966–67	1967–68	1968–69	1969–70	1970–71	1971–72	1972–73
Sex ♂							
Age-group							
0	26.6	17.7	21.5	16.7	5.3	9.2	8.4
1	50.1	19.9	27.8	21.1	28.4	18.9	15.2
2	19.3	4.0	23.1	11.6	8.7	10.9	6.0
3	3.2	6.3	3.4	0.1	2.4	2.7	2.6
Total	99.2	47.9	75.8	49.5	44.8	41.7	32.2
Sex ♀							
0	23.8	17.7	22.7	15.6	5.1	8.5	9.6
1	30.7	42.2	18.4	20.3	32.3	26.2	19.8
2	9.4	5.1	6.7	5.3	3.9	6.8	7.0
3	0.5	0.2	2.0	0.2	1.2	2.2	4.2
Total	61.4	65.2	49.8	41.4	42.5	43.7	40.6

population size is variable and controlled by extrinsic factors, minimizing the loss of production to nonpredatory mortality would be the best strategy.

In these lakes, the crayfish population is relatively stable. Size of the population is subject to intrinsic control as indicated by the life tables (Table 3). Thus maximizing production rather than minimizing production losses seems the best strategy to adopt.

Neither predator "allows for" production maximization before harvesting the crop. Production was maximized at age 1 (Table 6). The trap fishery harvested a cohort well after maximum biomass production was achieved. By increasing the harvest to include age 1 crayfish, the trap fishery could maximize production. However, since this would increase the stress on the l_x and m_x values of age 2 females, these effects would have to be monitored carefully.

The trout are prevented from utilizing either strategy. Since they prey only on the youngest age-class, once the crayfish are large enough the predator no longer has any effect on crayfish reproduction. In addition, while the numerical mortality of the 0+ age-group is on the order of 85–95%, trout at best consume 23% of the cohort (Gowing and Momot 1974).

Harvesting a prey population at the size at which cohort reaches maximum production can lead to unforseen consequences, depending on the relationship between prey size, the interaction between growth efficiency, and food utilization of size of prey being exploited. Kerr and Martin (1970) suggest that harvesting might be best carried out at the smallest practicable size. Where food type and growth efficiency of the prey change with the size of the prey, the size range selected for optimal exploitation should be the best compromise of small size and high growth efficiency obtaining at various stages in the life cycle of the species.

In crayfish, the major response in the production process is probably through survivorship and

egg production, rather than growth (Table 3) (Gowing and Momot 1974). Still their adult metabolism shows a great flexibility in response to available feeding conditions as a result of their polytrophic role in the community (Moshiri and Goldman 1969; Flint and Goldman 1975). Where food conversion greatly changes with size the effects of fishing would be greatly magnified (Paloheimo and Dickie 1970). Probably crayfish are more flexible in this regard than fish because of their ability to utilize a variety of food sources. So harvest might have less impact on the food conversion efficiency of crayfish populations. Hence they might lend themselves quite well to harvesting at the smallest practicable size, yet would have a high growth efficiency and adequate recruitment. Certainly more data on the food conversion efficiency of crayfish are necessary to resolve this question.

Thus we can say the crayfish population showed extreme resilience to certain types of stress caused by predation. This resilience came about through an adjustment of both the survivorship curves and egg production. The effects of any stress would depend greatly on whether or not any new stress resembled any existing natural stress to which crayfish are already well adapted. In this case the population was well adapted to handle additional stress.

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Population Differences in Rainbow Smelt, *Osmerus mordax*: Multivariate Analysis of Mensural and Meristic Data[1]

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COPEMAN, D. G. 1977. Population differences in rainbow smelt, *Osmerus mordax*: multivariate analysis of mensural and meristic data. J. Fish. Res. Board Can. 34: 1220–1229.

The phenetic relationships are investigated between 13 samples of sexually mature rainbow smelt, *Osmerus mordax*, from 12 collecting sites including representatives of anadromous and landlocked populations. Data on 32 mensural and meristic characters were obtained. Univariate and multivariate analyses revealed that the samples fell into three distinct groups composed of the anadromous, normal freshwater, and stunted freshwater populations. Mean values of the mensural and some meristic characters decreased across these three groups; some other meristics increased. It is doubtful whether the magnitude of the observed meristic variation represents solely a plastic environmental response.

The two freshwater stunted samples were 100% separable from the freshwater normal and anadromous samples using all the data, and 92.5 and 97.5% separable using one (total gill rakers) and all meristics, respectively. The identification success and other published biological data indicate that they fulfill the criteria for species recognition.

Between anadromous and normal freshwater groups 99.2% correct identification was achieved when all data were used. Using only one and two meristics (total gill rakers and total vertebrae), 89.1 and 91.4% correct identification was achieved, which suggests subspecific status for these two groups.

When the freshwater normal and anadromous groups were analyzed separately, more variation was seen within the freshwater group. Evidence of year-to-year variation was seen from the analysis of the anadromous samples and evidence for a genetic basis is presented.

Key words: *Osmerus mordax*, population, anadromous, freshwater stunted, variation, meristic, multivariate, taxonomy

COPEMAN, D. G. 1977. Population differences in rainbow smelt, *Osmerus mordax*: multivariate analysis of mensural and meristic data. J. Fish. Res. Board Can. 34: 1220–1229.

L'auteur étudie les relations phénétiques entre 13 échantillons d'*Osmerus mordax* ayant atteint la maturité sexuelle et provenant de 12 endroits d'échantillonnage, comprenant des représentants de populations anadromes et landlockées. Il a recueilli des données sur 32 caractères morphologiques et numériques. L'analyse unidimensionnelle et multidimensionnelle révèle que les échantillons se divisent en trois groupes distincts: populations anadromes, populations d'eau douce normales et populations d'eau douce naines. Les valeurs moyennes des caractères morphologiques et de quelques caractères numériques diminuent de l'un à l'autre de ces trois groupes; certains autres caractères numériques augmentent. Il est douteux que l'amplitude de la variation dans les caractères numériques représente seulement une réponse plastique à l'environnement.

Les deux échantillons nains d'eau douce peuvent être séparés à 100% à la fois des échantillons normaux d'eau douce et des échantillons anadromes en se basant sur toutes les données, et séparables à 92.5% et 97.5% en utilisant un (les branchicténies totales) et tous les caractères numériques, respectivement. Le succès de l'identification, de même que d'autres données publiées indiquent que les populations naines possèdent les critères suffisants pour qu'on lui reconnaissance le rang d'espèce.

On a pu séparer avec une exactitude de 99.2% les groupes anadromes et d'eau douce normaux en utilisant toutes les données. Avec un et deux caractères numériques (branchicténies totales et vertèbres totales), l'identification a été exacte dans 89.1 et 91.4% des cas, ce qui suggère un rang de sous-espèce pour ces deux groupes.

Analysant séparément les groupes normaux d'eau douce et anadromes, nous observons plus de variation au sein du groupe d'eau douce. L'analyse des échantillons d'eau douce révèle une variation d'année en année, et nous démontrons une fondement génétique.

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RAINBOW smelt, *Osmerus mordax*, is a wide ranging and commercially important fish. Populations of rainbow smelt may live either exclusively in freshwater or migrate seawards, where for part of their life they are found in brackish bays. A high degree of local variability is found between populations of this group to the extent that five eastern North American populations have previously been considered as separate species and have been considered together as a subspecies of the European smelt (McAllister 1963). Interpopulation studies have shown variation in spawning time, growth rate, food preference, morphometrics, meristics, and osteology (Kendall 1927; Rupp 1959; Rupp and Redmond 1966; Delisle 1969; Rembiszewski 1970). Further, freshwater smelt populations may consist of either stunted or normal individuals, and one lake may contain populations of both types. These sympatric populations have been called dwarf and giant, respectively (Delisle 1969). Anadromous populations are of normal size. The interpopulation diversity indicates that gene flow may be drastically curtailed, even between populations that are geographically close, and that the population is the functional unit (Ehrlich and Raven 1969) in smelt. Previous studies have tended to be univariate. No pattern of variation has emerged for the eastern North American smelt, and no consensus on the taxonomy has developed. This paper concerns itself with three questions. Do individual populations of smelt fall into recognizable groups? What are the levels of difference and possible taxonomic status between groups? What are the possible causes of the variation between and within groups?

Materials and Methods

Thirteen samples of smelt taken from 11 geographical areas were examined (Table 1). All samples except the one from Grand Bank were taken during the populations' spawning runs and were composed of sexually mature individuals. All samples except the two from Lake Heney, Quebec, were immediately frozen upon capture and shipped to the Marine Sciences Research Laboratory, St. John's, packed in dry ice.

Each specimen was thawed, weighed, sexed, aged, measured (standard length), and fixed in 10% neutralized Formalin. Twenty individuals were taken at random from each sample for further study. Morphometric measurements were taken to the nearest 0.1 mm using Helios dial calipers. The tip of the lower jaw was used as the anterior reference point. Vertebral counts, including the urostyle and dorsal and anal fin-ray counts, were made from X-ray plates (Kodak Industrial Type M, X-ray film). Age was determined using the "shiny line" scale method (McKenzie 1958). Measurements (Table 2) were made according to the methods described by Hubbs and Lagler (1947) and Berg (1948).

The discriminant function analysis and canonical analysis (Fisher 1936) were performed at the Newfoundland and Labrador Computer Services (I.B.M. 370/155) using the program BMD 07M (Dixon 1965). An intersample generalized distance matrix was computed from the 12 sets of coordinates derived from the orthogonal vectors. An unweighted pair group method (UPGM) cluster analysis (Sokal and Michener 1958) and minimum spanning tree (MST) (Gower and Ross 1969) were computed from the matrix. The positions of the arms of the branches were arranged with the aid of the MST. Minimum spanning trees were computed using programs supplied by Dr G. J. S. Ross (Ross 1969a, b, c). The other programs employed were written by the author.

Results and Discussion

GENERAL RESULTS

It was first necessary to determine whether the individual samples were identical or whether they fell into distinct groups whose interrelationships could be studied separately. The results of the discriminant function analysis indicated that the hypothesis that the 13 samples of smelt were homogeneous was highly improbable when 32 variables were included in the discriminant functions ($F(384, 2472) \simeq 11.71$, $P = <0.001$). This hypothesis was even highly improbable with only one variable (total gill rakers) considered ($P = <0.001$). The significance of each root was tested (Bartlett 1947) and the results are seen in Table 3.

As the samples did not appear to be the same, it was desirable to determine any relationships that might exist between them. Canonical analysis was performed and provided the graphic representation of the relations between the samples (Fig. 1). The first two canonical variates accounted for 85.1% of the variation (Table 3). The UPGM cluster analysis performed on the generalized distance matrix showed two principal clusters. These joined at the 19.3 level (Fig. 2) and consisted of the normal samples and the two "stunted" samples (L.H.S. and G.L.). The normal samples formed two subclusters, one containing anadromous fish, the other freshwater fish. The N.A.(69) and L.H.G. sample joined the "normal" cluster after the two subclusters had joined. However, the MST (Fig. 1) shows that these samples are obviously members of the anadromous and freshwater groups, respectively. The first two clusters to form (N.A.(70) — I.R. and L.R. — S.B.) contained samples taken from the same geographical area at about the same time and are referred to as nearest neighbours.

TABLE 1. Sample areas, dates, their abbreviations used throughout the text, number on which standard length and other basic data taken, minimum and maximum standard lengths and group to which sample assigned (A, anadromous; N, normal freshwater; S, stunted freshwater).

Sample area	Sample code	Date of capture	No.	Std. length (mm) Min	Std. length (mm) Max	Group
Norris Arm (Notre Dame Bay, Nfld.)	N.A.(69)	Apr. 12, 1969	200	163	216	A
Norris Arm	N.A.(70)	May 14, 1970	100	139	179	A
Chuff Brook (Sandringham, Bonavista Bay, Nfld.)	C.B.	June 5, 1969	100	121	163	A
Little River (Port au Port Bay, Nfld.)	L.R.	June 15, 1969	100	123	180	A
Smelt Brook (Port au Port Bay, Nfld.)	S.B.	June 15, 1969	100	121	172	A
Indian River (Notre Dame Bay, Nfld.)	I.R.	May 13, 1970	100	137	223	A
Grand Bank (Garnish River, Burin, Nfld.)	G.B.	Oct. 16, 1970	100	114	187	A
Lake Superior (Chequanagon Bay, Wis.)	L.S.	Apr. 23, 1970	100	111	196	N
Lake Huron (McKim Creek, Manitoulin Island)	L.H.	Apr. 29, 1970	100	105	153	N
Lake Erie (Morpeth, Ont.)	L.E.	Apr. 23, 1970	100	124	172	N
Lake Heney Giant (Lake Heney, Que.)	L.H.G.	Mar. 1967	40	157	206	N
Lake Heney Stunted (Lake Heney, Que.)	L.H.S.	May 1967	40	68	79	S
Green Lake (Maine)	G.L.	Apr. 27, 1970	100	71	82	S

The minimum and maximum standard length values for each sample (Table 1) indicated that there was no overlap between the stunted fish (L.H.S. and G.L.) and the others, even though 2-yr-old fish comprised 14% of the total normal sample. The means and standard deviations were then calculated separately for each of the three groups, anadromous, freshwater-normal, and freshwater-stunted (Table 2). The means of all the linear measurements from the anadromous fish were slightly larger than those of the normal freshwater group and approximately double the means from the samples of stunted fish.

The samples have been partitioned with the implication that they are distinct groups. The statistical significance of these groups has been discussed (Copeman 1973). From a more practical consideration, objects are more or less distinct depending on the success with which they are distinguished and assigned to their correct group. Individuals were assigned to a sample on the basis of the computed discriminant functions. When information from 32 variables had been considered (Table 4), 93.5% of the individuals were correctly identified to sample. If the nearest neighbours were combined, 96.5% were correctly

TABLE 2. Means and standard deviations (σ) in millimetres of characters for different groups.

Number[a] and character	Overall		Anadromous group		Normal freshwater group		Stunted freshwater group	
	Mean	σ	Mean	σ	Mean	σ	Mean	σ
1. Wt (g)	33.3	18.30	40.7	19.87	34.7	16.16	4.0	0.42
2. Age (yr)	3.1	0.67	3.3	1.64	3.2	0.73	2.0	0.0
3. Standard length	141.1	32.88	155.8	22.20	148.0	22.17	75.8	3.51
4. Anal fin to maxillary length	106.8	24.82	117.6	16.58	112.5	17.87	57.8	2.58
5. Dorsal fin to maxillary length	73.6	16.99	80.5	11.58	78.3	12.78	40.1	1.74
6. Pelvic fin to maxillary length	76.3	14.74	83.8	12.03	80.9	13.13	41.1	2.07
7. Pectoral fin to maxillary length	35.3	8.06	38.7	5.36	37.2	6.44	19.5	1.02
8. Posterio-ventral region length	42.1	10.01	46.1	7.16	45.0	7.75	22.1	1.50
9. Base of dorsal fin length	12.4	3.13	13.8	2.20	13.1	2.33	6.3	0.44
10. Ht of dorsal fin	21.6	4.57	23.8	3.16	22.3	3.54	12.5	0.88
11. Length of pectoral fin	20.5	4.32	22.4	3.26	21.5	3.10	12.2	0.86
12. Length of pelvic fin	17.3	3.84	19.1	2.75	17.8	2.78	10.0	0.55
13. Base of anal fin length	20.1	4.81	22.5	3.79	20.7	3.12	10.5	0.83
14. Ht of anal fin	12.7	2.67	13.4	2.01	12.6	2.36	7.0	0.46
15. Length from adipose fin to base of the tail	21.6	5.21	24.2	3.83	22.3	2.83	11.3	0.94
16. Depth of caudal peduncle	8.1	1.83	8.8	1.27	8.6	1.22	4.4	0.40
17. Length of head	35.4	8.24	38.9	5.41	37.2	6.58	19.3	0.90
18. Length of orbit	8.1	1.50	8.7	1.05	8.6	1.24	5.3	0.30
19. Length of snout	10.1	2.71	11.2	1.89	10.9	2.28	5.0	0.41
20. Interorbital width	8.2	2.32	9.2	1.69	8.6	1.67	3.8	0.33
21. Length of upper jaw	16.2	4.22	17.9	3.03	17.2	3.47	8.3	0.41
22. No. of pelvic fin rays	8.0	0.04	8.0	0.12	8.0	0.17	8.0	0.16
23. No. of anal fin rays	15.0	0.28	15.0	0.58	14.8	0.55	15.4	0.60
24. No. of pectoral fin rays	11.7	0.47	11.3	0.61	12.0	0.69	12.1	0.52
25. No. of gill rakers, upper arm	9.9	0.90	9.2	0.56	10.4	0.72	11.4	0.63
26. No. of gill rakers, lower arm	21.6	1.82	20.2	1.03	22.3	1.09	24.7	1.12
27. Total no. of gill rakers	31.5	2.70	29.4	1.38	32.8	1.50	36.0	1.36
28. No. of dorsal fin rays	10.1	0.29	9.9	0.42	10.3	0.48	10.3	0.51
29. No. of pored lateral line scales	16.9	1.38	17.5	1.82	16.9	2.34	15.2	2.19
30. No. of abdominal vertebrae	39.9	0.69	40.4	0.68	39.4	1.11	39.1	1.10
31. No. of caudal vertebrae	22.7	0.41	23.0	0.64	23.4	0.74	23.3	0.89
32. Total no. of vertebrae	62.6	1.08	63.4	0.84	61.9	1.47	61.4	1.32

[a]Used in Table 3 and Fig. 2.

identified. Correct identification for anadromous vs. freshwater decision was 99.2%, while the stunted fish were completely distinct (100%) from the normal fish with the inclusion of the second variable in the discriminant functions.

The levels of correct identification varied with the number of variables in the discriminant functions. These relationships are seen in Fig. 3. The order of the first five variables included in the discriminant functions was: total number of gill rakers, depth of caudal peduncle, weight, standard length, and length of orbit. For the anadromous–freshwater distinction, the 75 and 90% levels of correct identification were achieved with the inclusion of the first and fourth variables, respectively. If certain variables were selected to maximize the distinction between these two groups, it was possible to achieve the 90% level with the inclusion of only two variables (total gill rakers and total vertebrae).

DIFFERENCES BETWEEN NORMAL AND STUNTED POPULATIONS

The plot of the samples' means along the first two canonical axes (Fig. 1) indicated clearly that these two stunted samples were more than 16 SD from the normal ones along axis I and formed a distinct group. The relative positions of the anadromous, freshwater, and stunted population along axis I reflected the relationships seen with the various length measurements (Table 2). The anadromous group's means were the largest and the stunted group's the smallest. This indicates

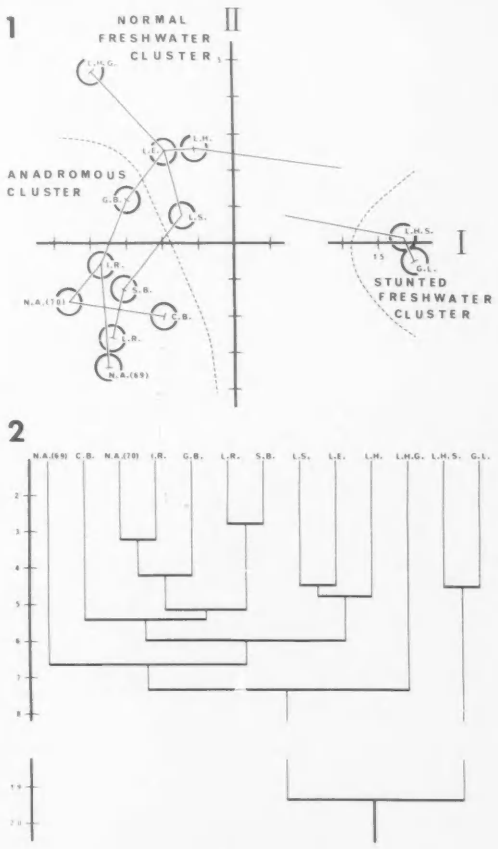
TABLE 3. Latent roots from solution of canonical equation, the cummulative percent variation (C%V) accounted for by each and the significance of the root.

No.	Latent root	C%V	χ^2	df	P
1	49.355	76.9	2760.28	384	< .0001
2	5.247	85.1	1833.42	341	< .0001
3	2.467	89.0	1400.12	300	< .0001
4	2.122	92.3	1106.09	261	< .0001
5	1.490	94.6	836.84	224	< .0001
6	1.059	96.2	621.08	189	< .0001
7	0.895	97.6	450.28	156	< .0001
8	0.560	98.5	299.10	125	< .0001
9	0.521	99.3	193.93	96	< .0001
10	0.183	99.6	94.75	69	.022
11	0.143	99.8	55.01	44	.124 (NS)
12	0.104	100.0	23.40	21	.423 (NS)
Total	64.146				

that the first variate is primarily a size vector, which is a common occurrence in multivariate studies (Blackith and Reyment 1971). In this case, the size vector may have important biological implications for the species.

It might be thought that the differences between the normal and stunted smelt are predominantly the result of the nonisometric growth common in fish (Martin 1949). The stunted fish were all 2 yr olds, whereas the majority of the normal fish were 3 and 4 yr. Two-year-old normal fish were also encountered (14%). However, these were always identified by the discriminant functions as belonging to the normal groups. Therefore, changes in form associated with different ages in the sexually mature smelt cannot be as strong a factor as that of normal–stunted, otherwise the above result would not have been obtained.

The taxonomic status of the two populations from Lake Heney has been considered by Delisle (1969), who concluded that they were distinct groups. The potential for the accumulation of genetic differences exists as these two sympatric populations spawn at different times and at different places and generally inhabit different regions of the lake. From the minimum length data (Table 1) the normal and stunted groups are completely distinguishable as there is no overlap in size of the spawning fish (minimum normal 105, maximum stunted 82 mm). A single meristic measurement (total gill rakers) permitted 92.5% correct identification of stunted individuals, and 97.5% correct identification was achieved when all the meristics alone were used (Copeman 1973). Kendall (1927) reported that Green Lake contained normal and stunted smelt. The present



FIGURES 1 AND 2

FIG. 1. Plot of samples means along the first two canonical axes and the minimum spanning tree. The circles around each sample mean have a radius of 1 SE (Seal 1968). FIG. 2. Dendrogram from an unweighted pair group method cluster analysis on the generalized distance matrix computed from the 12 sets of coordinates generated from the canonical analysis with 32 variables.

sample was from a stunted population as seen in the clusters of Fig. 1 and 2. The results of this work corroborates Delisle's findings and have shown that the relationships are maintained on the basis of a much wider geographical and temporal sampling.

Differences in size as well as gill raker and vertebral counts along with the sympatry and reproductive isolation strongly suggest that formal species recognition be accorded. Before this is done, it seems desirable to examine other lakes, especially for dwarf types, to see whether they fall reasonably well into one of the two categories.

TABLE 4. Identification of individuals in samples using 32 variables in the discriminant functions. Anadromous, normal freshwater, and stunted freshwater regions are enclosed by asterisks and nearest neighbours are set off. Sum of all rows is 20 and correct identification is seen as the summed diagonal.

	Individual assigned to													
Sample	N.A.(69)	C.B.	L.R.	S.B.	I.R.	N.A.(70)	G.B.	L.S.	L.H.	L.E.	L.H.G.	G.L.	L.H.S.	
N.A.(69)	18	0	1	0	1	0	0	0	0	0	0	0	0	
C.B.	0	20	0	0	0	0	0	0	0	0	0	0	0	
L.R.	0	0	17	3	0	0	0	0	0	0	0	0	0	
S.B.	0	0	3	17	0	0	0	0	0	0	0	0	0	
I.R.	0	0	0	1	16	1	2	0	0	0	0	0	0	
N.A.(70)	0	0	0	1	1	18	0	0	0	0	0	0	0	
G.B.	0	0	0	0	0	0	20	0	0	0	0	0	0	
L.S.	0	0	0	1	0	0	0	19	0	0	0	0	0	
L.H.	0	0	0	0	0	0	0	0	19	1	0	0	0	
L.E.	0	0	0	1	0	0	0	0	0	19	0	0	0	
L.H.G.	0	0	0	0	0	0	0	0	0	0	20	0	0	
G.L.	0	0	0	0	0	0	0	0	0	0	0	20	0	
L.H.S.	0	0	0	0	0	0	0	0	0	0	0	0	20	

DIFFERENCES BETWEEN NORMAL FRESHWATER AND ANADROMOUS POPULATIONS

The differences between normal freshwater and anadromous smelt populations were great enough to permit these to be readily identified as two groups that conform to Mayr's (1963) definition of subspecies, although presently lacking a formal trinomen. With the exception of the Grand Bank sample, anadromous smelt formed a cluster in the lower left quadrant (Fig. 1). The anadromous and freshwater groups were separable by a straight line. In the generalized distance dendrogram (Fig. 2), the anadromous and freshwater samples formed separate clusters that joined at the 5.9 level. Here, the G.B. sample was clearly seen as a member of the anadromous group. The N.A.(69) and L.H.G. samples were seen as the extreme cases of the anadromous–freshwater distinction (Fig. 1).

The differences between the anadromous and normal freshwater groups were evaluated by pooling the separate samples into the appropriate category and rerunning the analysis (Copeman 1973); the importance of meristic characters was seen. The three most successful variables incorporated into the discriminant functions were meristic. Total gill rakers permitted 89.1% correct identification and the addition of total vertebrae raised the level to 91.4%. Comparing the eleven meristic characters between these two groups, eight *t*-tests were highly significant ($P < 0.001$) and only one was not significant ($P > 0.05$).

As the number of meristic elements is determined before hatching in salmonoid fish (Taning 1952; Seymour 1956), the affected numbers should be determined while the eggs are still on the spawning grounds. Smelt eggs become attached to the substrate and complete development while attached (Soin and Unanyan 1964). Experimental studies indicate that temperature may be a major environmental modifier of meristic characters (Lindsey 1953, 1962; Barlow 1961; Lindsey and Ali 1965; Hubbs and Bryan 1973; Solemdal 1973). Temperature data were not available for

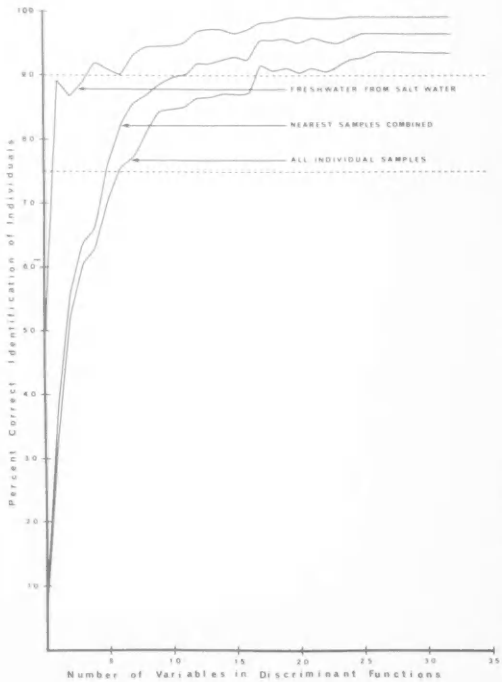

FRESHWATER FROM SALT WATER
NEAREST SAMPLES COMBINED
ALL INDIVIDUAL SAMPLES
Percent Correct Identification of Individuals
Number of Variables in Discriminant Functions

FIG. 3. The percentage of individuals correctly identified vs. the number of variables considered in the discriminant functions for different subdivisions of the identification matrices.

the localities and years that were of interest. However, in 1970 the range of spawning temperatures in the Great Lakes was 5.0–12.5°C, while in anadromous spawning sites the range was 9.0–12.5°C (Copeman 1973). This overlap of spawning temperatures of freshwater and anadromous samples was not reflected in the degree of overlap of means of meristic characters. The mean of each anadromous sample's total vertebrae was greater than that of any freshwater sample's. The anadromous group's mean was 1.5 more than the freshwater group's (Table 2). This is larger than the maximum difference, 1.37, obtained by Taning (1952) in his experimental studies on fish with similar numbers of vertebrae. The largest vertebral difference obtained between means of individual anadromous and freshwater samples was 2.85 in this study.

The situation was reversed with respect to total gill rakers in that each freshwater sample had greater values for that mean. The difference between group means was 3.4 and the maximum between sample means difference was 5.35. There is little to indicate that the degree of expression of either of these characters can be attributed to thermal modification. Rather, the differences are great enough to suggest genetic dissimilarity. If the meristic dissimilarities between the major smelt groups reflect primarily genetic differences, then selection appears to be working in one direction with axial elements and in the opposite direction with the dorsal and pectoral fin rays and gill rakers. This phenomenon has been seen in other salmonoids (Northcote et al. 1970; McCart and Bain 1974).

The mean generalized distance between anadromous and freshwater samples was 6.57. Delany and Healy (1966) working on island populations of white-toothed shrews found that a generalized distance > 8.2 corresponded to groups recognized previously as two species (Cranbrook and Crowcroft 1958). Although the results of my study are not directly comparable, as a different number of samples and variables were used, a number of the intergroup distances approach the 8.2 values. In addition, although there is temporal and geographic variation between the samples within the anadromous and freshwater groups, there was no overlap between them (Fig. 1) and nearly 90% of individuals and all populations could be assigned to their correct group on the basis of a single criterion (Σ G.R. $\leqslant 31$). It remains to be decided whether the anadromous population has given rise to several freshwater populations, which resemble one another because of parallelism, rather than common ancestry.

INTRAGROUP VARIATION

When anadromous and normal freshwater samples were analyzed separately, the results indicated that even close populations within major groups are distinct enough to permit a high level of success in identifying individuals. Within the freshwater and anadromous groups, 75% correct identification to sample could be achieved with two and five variables, respectively. Maximum identification success to sample for anadromous and freshwater fish were 93.6 and 98.8%, respectively (Copeman 1973). Calaprice (1971) has shown an improvement in identification success with an increase in the number of replicates used to compute the discriminate functions. This suggests that the populations within major groups may be even more distinct than was seen with results from these limited samples. Greater variance was found between the four freshwater samples than between the seven salt water samples, as indicated by the sum of the latent roots, 16.3 and 9.5, respectively. This result might have been predicted by reasoning that the individual

lakes would experience greater environmental variation than the Newfoundland marine area and therefore, the lake populations could be expected to show greater differences due to either selective environmental pressures or plastic responses.

Many good experimental studies have shown that environmentally induced meristic change is to be expected in response to temperature variation. There was a gradual decrease in mean vertebrae values from north to south, although the ranges were the about same, 60–64 for L.S. and L.H. and 61–63 for the L.E. sample. None of the intersample meristic comparisons were significant at $P = 0.05$, for the freshwater group. Generally, meristic variation was relatively nonsignificant between the normal freshwater samples. This was somewhat surprising in light of the differences in spawning water temperatures encountered (L.S. 5.0°C, L.E. 12.5°C). Genetic differences may exist and be counteracted by different environments, resulting in the phenetic similarily.

When the seven anadromous samples were analyzed separately, evidence of year-to-year variation was seen. The results of the analysis presented in Fig. 1 showed that the 1969 and 1970 anadromous samples were separated by canonical axis V. However, the analysis of only the anadromous samples showed that the major distinction along canonical axis I was the year of capture and 36.5% of the variation in the data was accounted for by this axis. This indicates that there was general and directional year-to-year variation. Similar to the situation seen within the freshwater group, mensural rather than meristic characters were of more use in distinguishing individual samples of anadromous smelt; i.e. morphometric characters appeared more sensitive to change between populations within a major environmental region.

Year-to-Year Variation Within a Population

Smelt populations vary phenetically from year to year. The existence and cause of these fluctuations in population parameters are critical to problems of stock identification, a cornerstone of fisheries management, especially if powerful multivariate methods are being used for discrimination problems. The interpopulation generalized distances between the consecutive Norris Arm samples (N.A.69 and N.A.70) and the sample from the same geographic region (I.R.) showed that the two 1970 samples were most similar (3.19) and the two annual samples from Norris Arm were least similar (6.05). A general size difference, allometric differences due to different age distributions, differences due to plastic responses to different environments, and genetic differences between populations have been considered as potential causes in this case.

The effect of the general size difference between the two samples (Table 1) was evaluated in two ways and the size-related effects were found to be relatively small. First, all mensural data were converted to ratios in an attempt to reduce any general size effect. The results of this canonical analysis did not appreciably differ from the ones obtained with raw data. A good fit for the Notre Dame Bay samples (N.A.(69), N.A.(70) and I.R.) was obtained by rotation and translation of canonical axis I and II from the transformed data to those from the raw data; the same generalized distance relationships were seen between the Notre Dame Bay samples with raw or transformed data (Copeman unpublished data). The second evaluation of the general size component was done by considering the effect of canonical axis I which often depicts the general size relationship as in this study (see Blackith and Reyment 1971 for summary). When the distance relationships between the Notre Dame Bay samples were recomputed without the coordinates from canonical axis I (the size component), the maximum decrease in distance was small (4%) and the same relationships between these samples were seen in the new distance matrix. Therefore, the "general size axis" contributed little to the differences between these samples.

Any allometric change in these sexually mature fish was relatively small compared to the differences between populations. The N.A.(69) sample contained the greatest proportion of 4 yr olds (59%) encountered with the anadromous samples. If 4-yr-old smelt had a characteristic form, it would have been expected that all 4-yr-old anadromous fish would have been assigned to this group. This did not happen (Table 4). On the other hand, two 4 yr olds from the N.A.(69) sample were incorrectly assigned to the identified L.R. and I.R. groups. These samples were composed predominantly of 3 yr olds, 70% and 65%, respectively. Therefore, changes in shape with age (3 to 4) do not appear to contribute greatly to the variation.

It might be intuitively argued that more genetic similarity exists between yearly samples of a single population than between distinct populations, and differences between yearly samples would be expected to result from plastic responses. Meristics in fish may be modified by environmental factors, principally temperature, during the early stages of development (Taning

1952; Lindsey 1953, 1962; Seymour 1956; Barlow 1961; Lindsey and Ali 1965), thereby adding weight to the argument that interpopulation differences are largely the result of environmental modification of phenotype. However, effects of spawning temperatures were not reflected in vertebral counts when the anadromous and freshwater groups were examined. Evidence for this genetic similarity has been seen in shad meristics (Hill 1959; Carscadden and Leggett 1975).

In natural populations of species with high reproductive potential, selection may be more important in determining the phenotype than might be expected, solely on the results of experimental studies or on species with relatively few offspring. The evidence for phenotypic selection rests on logical probablistic considerations as well as the close agreement seen between phenetic and enzymatic patterns of variation. Smelt may produce 42,000 eggs per female (Legault and Delisle 1968), of which only 1% may survive to the posthatching stage (McKenzie 1947; Rupp 1965). The resulting 420 larvae could suffer 50% mortality 8 times and still produce adults for spawning in 2–3 yr time. Assuming a certain degree of genetic variation, a tremendous potential for selection exists. Since only 0.005% of smelt eggs result in adults, even subtle selective advantages could be important in determining resulting allelic frequencies and phenotypes.

Populations may be considered genetically different due to different frequencies of alleles common to all populations. Electrophoretic investigations of enzyme systems has increased our capacity to obtain genotypic data (Gould and Johnston 1972). The analysis of esterase polymorphism data (Copeman 1973) from the three Notre Dame Bay samples showed the same pattern of relationships as the morphometric and meristic data. Therefore, if the esterase data can be taken as reflecting the genomes, then the similarity in the patterns of relationship, resulting from the two different data sources, suggests that the phenetic interpopulation differences seen at the finest levels could well have a genetic base.

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A Multiple Opening and Closing Plankton Sampler Based on the MOCNESS and N.I.O. Nets[1]

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SAMEOTO, D. D., L. O. JAROSZYNSKI, AND W. B. FRASER. 1977. A multiple opening and closing plankton sampler based on the MOCNESS and N.I.O. nets. J. Fish. Res. Board Can. 34: 1230–1235.

A multiple net zooplankton sampler with 10 1-m² nets was designed and built using the principles incorporated in the N.I.O. and the MOCNESS zooplankton samplers. The main differences between this net and others are the use of a depressor as part of the design of the sampler and the use of a ridge frame and cables to form the sampler body. The depressor enabled the sampler to be towed at speeds up to 6 knots while still maintaining a wire angle of <45°.

Key words: multiple net zooplankton sampler, net depressor

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Utilisant les principes incorporés dans les échantillonneurs de zooplancton de la N.I.O. et de MOCNESS, nous avons construit un échantillonneur de zooplancton à filets multiples, soit 10 filets de 1 m². Ce filet se distingue des autres filets surtout par l'emploi d'un dépresseur comme composante de l'échantillonneur, et d'un châssis en arête et de câbles pour former le corps de l'échantillonneur. Le dépresseur permet de touer l'échantillonneur à des vitesses allant jusqu'à 6 nœuds, tout en maintenant un angle de fune <45°.

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DURING the last 4 yr we have been studying acoustic scattering layers caused by zooplankton in the Gulf of St. Lawrence (Sameoto 1976). For the extensive biological sampling we used opening and closing bongo nets (McGowan and Brown 1966), but these proved inadequate because the study required a greater number of samples to be taken within a short period of time (30–60 min) than was possible with the bongo nets. What we needed was a net that could take several independent samples during a single tow at any desired depth on command. (See Frost and McCrone 1974 and Wiebe et al. 1976 for a more complete discussion of the advantages of a multiple opening and closing plankton net.)

We decided to construct a multiple net plankton sampler using concepts from the MOCNESS (Wiebe et al. 1976) and N.I.O. net (Baker et al. 1973). We needed a sampler that could be towed at speeds up to 6 knots and had a high degree of vertical stability over the speed range. The sampler had to be very robust and compact, since it would be used on a variety of ships from small inshore craft of <20.2 m (65 ft) to large ocean-going research ships. Because of the speed and stability requirements, we decided to incorporate a depressor into the design of the sampler. In addition to the electronics needed to open and close the nets, provisions were made to obtain data on the net depth, net pitch and roll, and water temperature.

Net Construction

The sampler has 10 nets with a mouth opening of 1 m² attached to 11 horizontal bars made from 33-mm² rectangular steel tubes. The plankton nets are attached to the bars by 12-mm-diam steel rods that pass through the collar of the nets and through three steel brackets on the back of

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the horizontal bars. Each bar holds the top part of the net below the bar and the bottom part of the net above the bar (Fig. 1 and 2). The bars are attached on both ends to 1-cm-diam steel cables (Fig. 2 and 3) and move freely on the cables. Each bar is attached to the release mechanism when the net is loaded before opening by a 5-mm-diam cable (I, Fig. 3) that hooks on the release mechanism (C, Fig. 3) with the other end secured to the center of the bar. The lengths of the cables are such that the bottom bar supports the weight of all the bars above it. As each bar falls when a net is opened the remaining bottom bar supports all the bars above it. This system

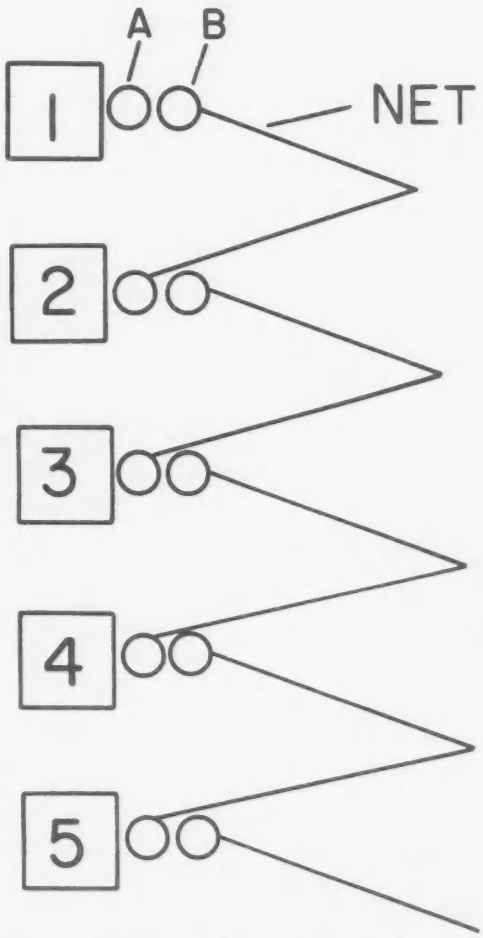

FIG. 1. Diagrammatic representation of the way the nets are attached to the first five horizontal steel bars. The attachment is the same for all bars. A and B are rods that hold the net to the horizontal bars.

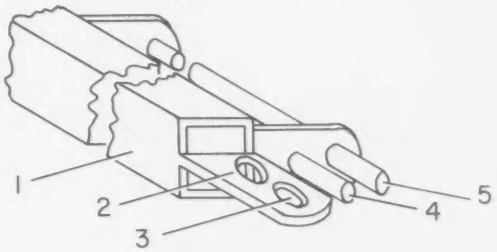

FIG. 2. End of a horizontal steel bar (1) showing method of attaching the bar to the two vertical cables. (2) hole for the 1-cm-diam cable; (3) hole for the 7-mm-diam cable; (4) steel rod used to hold the bottom part of the net above the bar; (5) steel rod used to hold the top part of the net below the bar.

was used to reduce friction on the cam of the release mechanism by having only one lever exerting a force on the cam at any time. The sides of the nets are attached to the vertical cables by Gibbs stainless steel snap swivels.

The release mechanism is a series of levers that provide a 12:1 mechanical advantage, held in place by a cam turned by an electric motor (E, Fig. 3). When the cam turns 20° it releases one of the levers. As the lever pivots on its axle it releases a cable (I, Fig. 3) that holds up the lowest horizontal bar and net. The bar and net then fall vertically by the force of gravity and a net is pulled open at the same time as one net is closed. The bars fit together tightly because the bottom bar holds up the weight of all the bars above it, thereby preventing contamination before the net was opened. After the net is closed the weight of the horizontal bars again ensured a close fit between the bars and prevented contamination. Side curtains were not put on the sampler to prevent contamination through the side folds of the nets when they were closed. The openings of the folds were only 1 or 2 cm high. During tests for contamination when the net was towed closed for approximately 1 h at speeds of 4 knots there were never any large forms of zooplankton present in the cod ends and very few specimens of the smaller species of copepods. Since our main concern was the study of macrozooplankton slight copepod contamination was not a problem. If one was studying the distribution of rare or scarce species of zooplankton, then the precaution of side curtains would be advisable.

When all the nets are released and the frame is brought to the surface, it is hoisted on the deck by hooking a lifting cable through the two loops of 7-mm-diam wire (D, Fig. 3). As the boom on the ship lifts the hook and pulls on the loops of

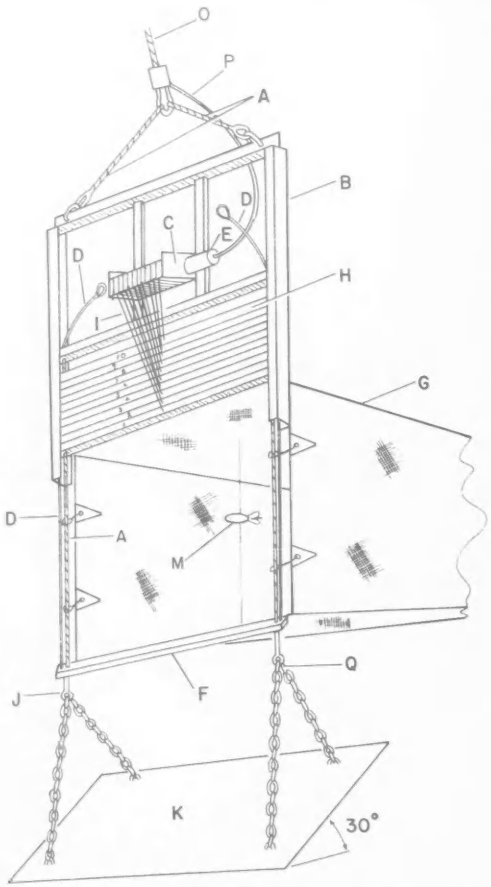

FIG. 3. The entire sampler from the front view excluding the environmental sensors that are attached to the upper frame. A, 1-cm-diam steel cable; B, aluminum frame; C, release mechanism consisting of cam and levers; D, 7-mm-diam steel cable; E, electric motor; F, steel bar; G, plankton net; H, steel bar (there are 10); I, 5-mm-diam steel wire (there are 10, one on each bar); J, steel eyebolt attached to cable A to which depressor is attached; K, steel depressor; M, flowmeter; O, 1-cm-diam conductor and tow cable; P, electrical conductor to motor; Q, weak-link strap.

wire it pulls up the bottom bar (F, Fig. 3) on which the 10 bars with the nets are resting. The cables (A, Fig. 3) are held tight by the weight of the depressor when the sampler is suspended in air. The bars and nets move freely up the 1-cm-diam cable and through the two channeled legs of the frame (B, Fig. 3) and into a position where they are ready to be loaded. The positions of the 10 bars that the nets are attached to during the sampling operation are shown in Fig. 4. The net is loaded as soon as it is taken from the water and before the samples are removed from the plankton buckets. The loading of the bars to the release mechanism takes about 2 min. The nets were then washed down and plankton buckets emptied. The total time needed to reload the 10 nets and remove the samples was about 20 min.

The ridged frame of the sampler (B, Fig. 3) was made of heavy gauge channel aluminum (45 mm wide × 73 mm deep × 7 mm thick). The frame was 122 cm wide and 147 cm high. The distance from the bottom of the frame to the attachment of the depressor was 100 cm. The total weight of the frame, nets and depressor in air was approximately 180 kg.

The depressor was made of a 3-mm-thick steel

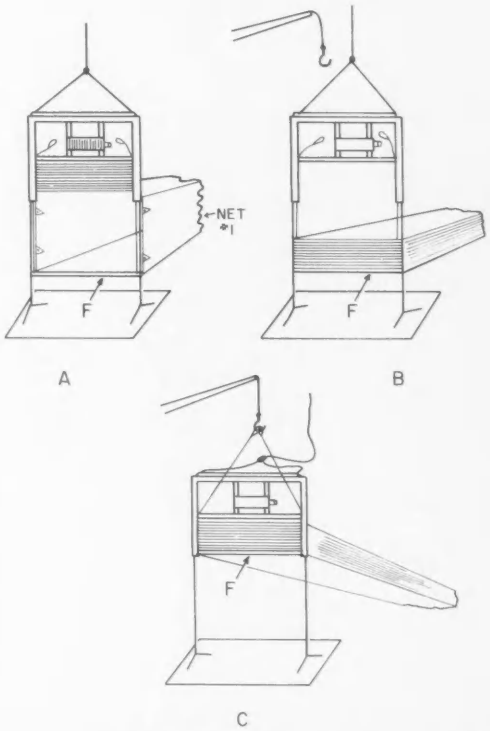

FIG. 4. A, The sampler as it looks being put over the side of the ship for the first sample. Net 1 is open as it goes into the water. B, The position of the 10 horizontal bars after all 10 nets have been opened and closed and the sampler has been taken out of the water and is hanging free. C, Method by which the 10 bars are raised into position to be loaded to the release mechanism. In this position the weight of the sampler is on the hook. F is the bottom bar to which the two loops of wire are attached.

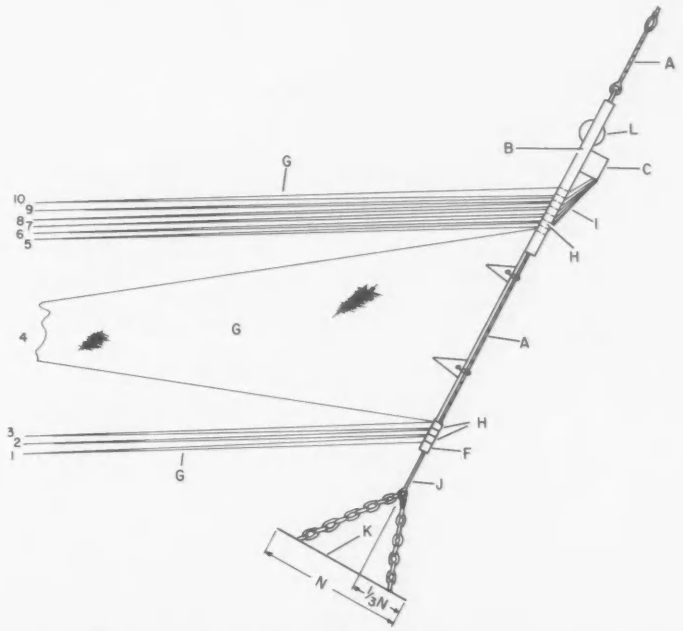

FIG. 5. Side view of sampler as it looked while being towed. Net 4 is open, nets 1–3 have been opened and closed. The capital letters refer to the same parts of the net as in Fig. 3; L, the pitch and roll meter attached to the frame; N, length of the depressor.

plate (125 × 155 cm) bolted to a steel frame. The depressor was held to the 1-cm-diam cable by two eyebolts attached to chains on the depressor (Fig. 3 and 5). The most important feature of the depressor was that it was suspended from the frame in such a way that a line projected downward from the frame would strike the depressor plate at a point one third of the width from the leading edge (Fig. 5). Weights were added to the front of the depressor to counter the greater weight behind the pivot joint (J, Fig. 3). It was found best to have enough weight (64 kg) to cause the front of the depressor to point down when the net was suspended in the air. This ensured that the depressor would bite into the water when it was lowered.

When the depressor is in the water and being towed it is approximately at an angle 30° from the horizontal (Fig. 5). A safety strap is attached between the eyebolt and chains on one side of the depressor. This strap has a breaking strength of 900 kg. This means that when the force on the depressor exceeds 900 kg the strap will break and the depressor will hang free from the other cable. The breaking force of the towing line (9.5-mm-diam conductor cable) was 5443 kg. This safety strap is needed when the net is towed in a high sea where forces on the depressor may exceed the breaking strength of the towing cable.

The various environmental sensors were attached to the frame above the release mechanism (not shown in Fig. 3). In the future, sensors for salinity and light and microprocessors to provide information on total water filtered during the tow will be added.

The net is opened by pushing a button switch on the deck control unit that generates a pulse that is transmitted down the conductor cable to the underwater unit. A trigger circuit is activated by the pulse that causes the stepping motor to turn the cam two 10° steps, thereby releasing a cable holding one of the nets. The motor, a Ledex model 21636-023, developed 43 g-mm of torque and required two 6-A current pulses to step it 20°. These current pulses are supplied by discharging two 15000-μF capacitators 500 ms apart. The capacitators are charged from a 28-V supply from the deck unit. By using capacitators we were able to make the underwater unit smaller than would have been possible had batteries been used. When a bar is released a switch is momentarily closed, incrementing a counter in the deck unit

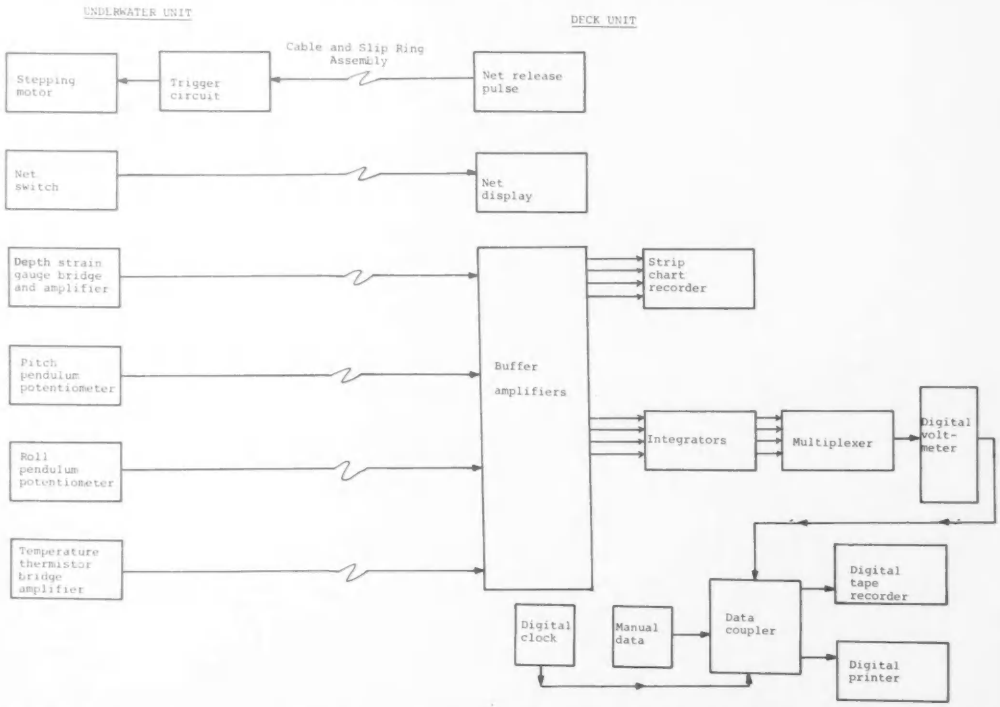

FIG. 6. Schematic diagram of the electronic components of the sampler. The lines connecting the deck unit with the underwater unit represent the conductors within the 9.5-mm-diam conductor cable.

that indicates which net is opened or closed. A schematic diagram of the electronic controls is given in Fig. 6.

Sensors on the sampler monitored temperature, depth, pitch and roll. The precision of the sensors were: temperature ± 0.02°C with an accuracy of 0.05°C; the pitch and roll ± 0.2°. This degree of precision was obtained from the digital read out. However, the strip chart recorder reduced precision for temperature to ± 0.5°C and pitch and roll to ± 1°. The pressure was precise to ± 0.5% of the full scale of 250 m. The flowmeters were precise to ± 1% of the actual flow. The DC output voltage of the sensors was transmitted up the cable to buffer amplifiers which output to a strip chart recorder and four integrators. The purpose of the integrators was to scale the input voltages to engineering units such as degrees. A multiplexer scanned the inputs at a predetermined interval. A digital voltmeter was used as the analog to digital converter. The data coupler accepted digital data from the voltmeter, clock, and manual data panel and output these data on a digital tape recorder and printer.

Net Performance

The angles of the mouth of the net at different towing speeds measured by the pitch and roll meter are given below. There was no significant roll to the net at any of the speeds. The depth variation of the net during a tow was very small at all speeds tested; it was a fraction of a metre once the ship's speed was stable.

Speed *knots*	Net angle degrees from the vertical	Line tension *kg*	Filtering mouth area m^2	Mouth area to surface area ratio
2.0	10	317	0.98	10.20
3.0	24	408	0.91	10.99
4.0	32	616	0.85	11.76
5.0	38	889	0.79	12.66
6.0	44	1224	0.72	13.89

The mouth area to surface area ratio of the nets was 1:10 for 243-μm mesh. General Oceanics model 2030 digital flow meters were tied in the mouth of each of the nets. The meters did not turn when the nets were closed because the fabric of the net held the propeller of the meter. A series

of 10-min tows was made with the nets closed to test the meters. The maximum number of revolutions recorded was 30; normally, 20,000 revolutions would have been recorded. A comparison of the flow through the net and outside of the net was made at 5 knots using the 243-μm nets. There was no significant difference in the flow rate during a 10-min tow. Normally, we do not tow the 243-μm net above 4 knots. Therefore, these nets were filtering nearly 100% of the water at 4 knots during the short tows. The mouth to surface area ratio as stated above was 1:10 assuming a 1-m^2 mouth opening. But as the net was towed, the opening was reduced as the angle of the net increased, which meant that as the speed increased the mouth to surface area ratio increased.

Due to the depth stabilizing effect of the depressor we were able to work in seas estimated to have a wave height of 5 m. Beyond this height the safety strap was in danger of breaking when the sampler was at a depth shallower than 50 m. At depths below 50 m the towing line acted as a shock absorber and tows could be made in rougher seas.

The frame of the sampler and all metal parts were painted a dull black and the nets were dyed a dark blue color to reduce any animal avoidance of the sampler that resulted from the animals seeing the net approaching. Using the 243-μm mesh nets we have captured a wide range of copepod species and fish larvae, euphausiids over 40 mm long and shrimp up to 90 mm long. A shock wave created by the 10 horizontal bars probably warned zooplankton of the presence of the net, but to what extent this helped animals avoid the net we cannot say; in the future we will streamline the sampler to minimize possible effects of the shock waves.

At towing speeds of 2.0 knots or less, few euphausiids (primarily *Meganyctiphanes norvegica*) were caught when the high frequency sonar indicated the euphausiids were abundant. When the speed was increased to 3.5 or 4.0 knots, large numbers of euphausiids and shrimp were caught at the same depth and location. At speeds of 6.0 knots the catches were not noticably different from those at 3.5 knots. This indicated that at 2.0 knots or less these large euphausiids (over 30 mm length) were able to avoid the net. There were no significant differences in the catch of copepods between tows of 2.0 and 6.0 knots.

Over 300 samples have been taken without a single malfunction of the release mechanism.

Acknowledgments

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Electrophoretic Distinction of Rainbow Trout (*Salmo gairdneri*), West-Slope Cutthroat Trout (*S. clarki*), and Their Hybrids

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REINITZ, G. L. 1977. Electrophoretic distinction of rainbow trout (*Salmo gairdneri*), west-slope cutthroat trout (*S. clarki*), and their hybrids. J. Fish. Res. Board Can. 34: 1236–1239.

Rainbow trout (*Salmo gairdneri*), west-slope cutthroat trout (*Salmo clarki*), and their F_1 hybrids were electrophoretically examined for 13 different proteins. Of the 13 proteins, only phosphoglucose isomerase (PGI) proved to be a reliable biochemical marker for the distinction of genetically pure samples of the two species. Only PGI provided an accurate means of identifying F_1 hybrids between the species. This information could possibly be used to facilitate the stabilization and restoration of native populations of west-slope cutthroat trout in western Montana.

Key words: rainbow trout, west-slope cutthroat trout, hybridization, electrophoresis, biochemical marker, phosphoglucose isomerase (PGI)

REINITZ, G. L. 1977. Electrophoretic distinction of rainbow trout (*Salmo gairdneri*), west-slope cutthroat trout (*S. clarki*), and their hybrids. J. Fish. Res. Board Can. 34: 1236–1239.

Nous avons dosé par électrophorèse 13 protéines différentes chez la truite arc-en-ciel (*Salmo gairdneri*), la truite fardée (*S. clarki*) du versant occidental et leurs hybrides F_1. Des 13 protéines, seule la phosphoglucose isomérase (PGI) s'est avérée une marque biochimique fiable permettant de distinguer des échantillons génétiquement purs des deux espèces. Seule la PGI permet d'identifier avec précision les hybrides F_1 entre les espèces. Il serait peut-être possible d'utiliser cette information pour faciliter la stabilisation et le rétablissement des populations indigènes de truites fardées du versant occidental dans le Montana occidental.

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THE west-slope cutthroat trout (*Salmo clarki*) was described in Pacific Railroad surveys of 1853–55 as inhabiting all waters in the mountainous regions of western Montana. Presently the distribution of "pure" native west-slope cutthroat trout is restricted to small relict populations in the extreme headwaters of mountain streams. This decline in the range of the west-slope cutthroat trout can be attributed to the introduction of several exotic species of trout in streams throughout Montana (Hanzel 1960). Rainbow trout (*S. gairdneri*) and brown trout (*S. trutta*) were both introduced into Montana in 1891 and brook trout (*Salvelinus fontinalis*) were introduced in 1894 (Hanzel 1960). All three of these species have successfully competed for habitat with the west-slope cutthroat trout. However, due to the widespread stocking of rainbow trout and the similarity of feeding habits of the rainbow and cutthroat trout (Brown 1971) and the production of viable hybrids between rainbow and cutthroat trout, the introduction of the rainbow trout has been the most important single factor in the decline of pure populations of native west-slope cutthroat trout in western Montana.

Programs designed to stabilize and possibly expand remanent populations of this subspecies of cutthroat trout native to western Montana have not been implemented because of the difficulty of detecting introgressive hybridization using conventional morphological means of classification. Aspinwall and Tsuyuki (1968) stated that species identification by the use of morphological criteria has proven unsatisfactory in areas where species hybridize, particularly when the hybridizing species are morphologically similar as is the case with rainbow and west-slope cutthroat trout. Therefore, to successfully stabilize and restore remanent populations of west-slope cutthroat trout in western Montana some additional means of hybrid identification is necessary.

Nyman (1970) reported electrophoretic techniques to be superior to the use of morphological

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characters in the identification of F_1 hybrids between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*). Numerous other studies have successfully used starch-gel electrophoresis as a means of species and hybrid identification (Abramoff et al. 1938; Tsuyuki and Roberts 1965; Aspinwall and Tsuyuki 1968). Therefore, this study was designed to identify any species-specific biochemical markers for the distinction of west-slope cutthroat trout, rainbow trout, and their hybrids with the use of starch-gel electrophoresis.

Materials and Methods

Six distinct populations of west-slope cutthroat trout were sampled to electrophoretically characterize this species. Of these six samples, one consisted of 103 west-slope cutthroat trout taken from the Jocko River State Trout Hatchery, Arlee, Montana. The west-slope cutthroat trout maintained at this hatchery were derived from eggs taken from Hungry Horse Creek which feeds into the Hungry Horse Reservoir in northwestern Montana. Other samples of approximately 30 west-slope cutthroat trout were taken from each of the following five streams located in northwestern Montana: Alice Creek (T16N, R7W, Sec 14D), Bear Trap Creek (T15N, R6W, Sec 27C), Shaue Gulch Creek (T15N, R6W, Sec 21B), Beaver Creek (T15N, R9W, Sec 32A), and Poor Man Creek (T13N, R8W, Sec 8C).

Tissue samples from over 2000 rainbow trout of three different strains maintained at the Fish Genetics Laboratory (FGL), Beulah, Wyoming, were used to electrophoretically characterize rainbow trout. An additional sample of 30 rainbow trout was obtained from the Jocko River State Trout Hatchery.

Hybrid crosses were made at the Jocko River State Trout Hatchery between 33 west-slope cutthroat trout females and 15 rainbow trout males. The carcasses of these fish were sent to the FGL for electrophoretic analysis. Eggs from this hybrid cross were shipped to the Leadville NFH, Leadville, Colorado, where they were reared to 6 mo of age. A sample of 25 of these hybrid trout was then shipped live to the FGL for electrophoretic examination.

All tissue samples were subjected to electrophoretic examination within 1 wk after collection. Samples of white muscle and liver were placed in 12 × 75-mm glass tubes in a ratio of 2 parts tissue to 1 part distilled water. The samples were then homogenized with a glass rod, centrifuged at 2500 rpm (1200 × *g*) for 10 min, and stored at −20°C.

Horizontal starch-gel electrophoresis was performed in the manner described by Utter et al. (1974). Buffer systems used and the proteins they best resolved are described in Table 1.

Staining procedures used followed those suggested by Shaw and Prasad (1970) and Selander et al. (1971), directly or with certain modifications except for that of tetrazolium oxidase, which was detected as achromatic zones on gels stained for sorbitol dehydrogenase.

Results

Of the 13 different proteins examined, AAT, ME, and XDH (see Table 1 for abbreviations) were expressed as single nonvariant bands with identical electrophoretic mobility in both rainbow trout and west-slope cutthroat trout. Table 2 lists the tissues examined for a specific protein. MDH, MP, LDH, PGM and TO were polymorphic in both species with all variant forms of these proteins expressed in west-slope cutthroat trout also being found in rainbow trout. Significant phenotypic frequency differences existed between the species for all five of these proteins. αGPD was fixed in west-slope cutthroat trout for the allele most common in rainbow trout. Some variant forms of IDH were unique to either rainbow trout or west-slope cutthroat trout with other forms being common to both. However, the rapid deterioration of IDH in many of the liver samples prevented a precise characterization of west-slope cutthroat IDH phenotypic frequencies.

Although both esterase (Es) and sorbitol dehydrogenase (SDH) appear to have banding patterns distinct between the two species, their genetics are not fully understood at this time. Therefore, no further mention of these two systems will be made.

TABLE 1. Buffer systems used for starch-gel electrophoresis.

Buffer system	Proteins best resolved by given system
1. After Ridgway et al. 1970. Electrode buffer — LiOH 0.1 M, H_3BO_4 0.3 M, pH 8.3. Gel buffer — Tris 0.03 M, citric acid 0.005 M, pH 8.0. Use 99% gel buffer and 1% electrode buffer for making gels. Electrode buffer undiluted in electrode trays.	Phosphoglucose isomerase (PGI), Lactate dehydrogenase (LDH), Sorbitol dehydrogenase (SDH), Xanthine dehydrogenase (XDH), αGlycerophosphate dehydrogenase (αGPD), Tetrazolium oxidase (TO) Phosphoglucomutase (PGM)
2. After Wolf et al. 1970. Stock solution — Na_2HPO_4 0.1 M with pH adjusted to 6 5 with 0.1 M NaH_2PO_4. Dilute stock solution 1:10 for gel, use undiluted in electrode trays.	Esterase (Es), Malate dehydrogenase, NADP dependent (ME)
3. After Shaw and Prasad 1970. Stock solution — Tris 0.155 M, citric acid 0.043 M, pH 7.0. Dilute 66.7 mℓ of stock solution to 1 ℓ for gel, use undiluted for electrode trays.	Isocitrate dehydrogenase (IDH), Malate dehydrogenase, NAD dependent (MDH)
4. After Selander et al. 1971 Stock solution A — 0.03 M LiOH, 0.19 M H_3BO_4, pH 8.1. Stock solution B — 0.05 M tris, 0.008 M citric acid, pH 8.4. Use 1 part A to 9 parts B for gel. Use stock solution A undiluted for electrode trays.	Aspartate aminotransferase (AAT), Muscle protein (MP)

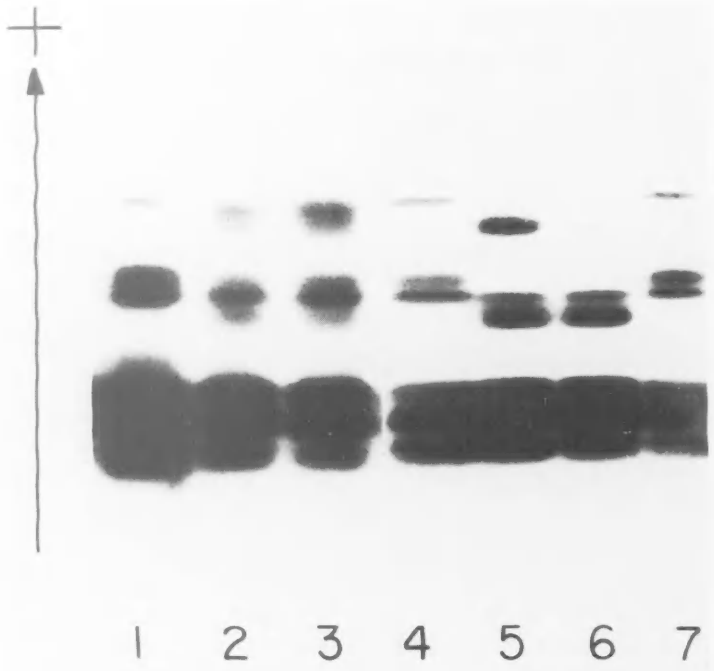

FIG. 1. Composite zymogram of phosphoglucose isomerase from west-slope cutthroat trout (*Salmo clarki*) (5 and 6), rainbow trout (*S. gairdneri*) (1, 4, and 7), and hybrid trout (2 and 3). Phenotypes: (1, 4, and 7) ABC; (2 and 3) AA^{w}BC; and (5 and 6) A^{w}A^{w}BC. Position of dimeric bands ordered from the anode to the cathode is AA, A^{w}A, A^{w}A^{w}, AB, AC and A^{w}B (at the same position), A^{w}C, BB, BC, and CC.

TABLE 2. List of the tissues examined for specific proteins.

Proteins	Liver	Muscle
Lactate dehydrogenase	×	
Sorbitol dehydrogenase	×	
Xanthine dehydrogenase	×	
Tetrazolium oxidase	×	
Esterase	×	
Isocitrate dehydrogenase	×	
Malate dehydrogenase, NADP dependent	×	
Malate dehydrogenase, NAD dependent	×	×
Phosphoglucose isomerase		×
αGlycerophosphate dehydrogenase		×
Phosphoglucomutase		×
Asparate aminotransferase		×
Muscle protein		×

PGI was fixed in west-slope cutthroat trout for a six-band pattern which was distinct from any pattern observed in rainbow trout (Fig. 1). Table 3 gives breeding data for PGI collected from rainbow trout of the Spring Standard strain maintained at the FGL. All hybrid trout examined for PGI expressed a nine-band pattern (Fig. 1) instead of the expected 10-band pattern because of the identical positions of the A^{w}B and AC dimeric bands.

Discussion

For a protein to be useful in the electrophoretic distinction of species and their hybrids, a variant form must be present in a high frequency in the second species. This variant form must be electrophoretically distinct from the form common to the second species. Ideally, a variant form of the protein would be fixed in one species and totally absent from the second species, thus constituting a species-specific marker. For accurate identification of F_1 hybrids, the electrophoretically distinct forms of protein found in the different species must be inherited as the combination of parental banding patterns. Of the 13 proteins examined in this study, only PGI met these criteria.

TABLE 3. Observed frequencies and (in parentheses) expected frequencies (assuming Mendelian inheritance) for phosphoglucose isomerase (PGI) in rainbow trout (*Salmo gairdneri*).

Parental genotypes		Progeny genotypes		
male	female	ABC	ABB′C	AB′B′C
ABC	ABB′C	11(10)	9(10)	
ABC	ABB′C	9(10)	11(10)	
ABB′C	ABC	9(10)	11(10)	
ABB′C	ABC	7(10)	13(10)	
ABB′C	ABB′C	4(5)	12(10)	4(5)
ABB′C	ABB′C	7(5)	9(10)	4(5)

Avise and Kitto (1973) and Schmidtke et al. (1975) suggested that three loci code for dimeric PGI in rainbow trout. Breeding data presented in Table 3 agree with this model. It would appear that *PGI-1*, like *PGI-2*, is fixed for alleles with electrophoretically identical products in rainbow trout and west-slope cutthroat trout. However, an allele for *PGI-3* was fixed in the west-slope cutthroat trout sampled which was not present in the rainbow trout sampled. Also PGI patterns in the hybrid trout were as expected for a dimeric molecule coded for at three loci with one locus having two alleles present. Therefore, any of the rainbow trout, west-slope cutthroat trout, or their F_1 hybrids examined in this study could have been classified as such, solely on the basis of their PGI phenotype.

Whether these differences in PGI phenotype hold true for all members of *S. gairdneri* and the subspecies of *S. clarki* examined in this study is impossible to say. To be able to do so with certainty would require sample sizes beyond reason for most studies. However, in view of the results of this study, it would be reasonable to assume that the "purity" of a population of west-slope cutthroat trout could be better judged by the use of both biochemical and morphological characters than by the use of either alone. With such information, sound management practices could then be implemented to preserve and restore remanent native populations of west-slope cutthroat trout in western Montana.

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Carbon Budgets in Lake Ontario

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CHARLTON, M. N. 1977. Carbon budgets in Lake Ontario. J. Fish. Res. Board Can. 34: 1240–1241.

A previous carbon budget for Lake Ontario appeared to balance because primary production was included as an input to the lake. Actually, the calculated CO_2 losses to the atmosphere cause yearly outputs to be much higher than inputs. The assumption that these CO_2 losses are a direct result of primary production is not consistent with other data.

Key words: carbon budget, primary production

CHARLTON, M. N. 1977. Carbon budgets in Lake Ontario. J. Fish. Res. Board Can. 34: 1240–1241.

Un budget de carbone calculé antérieurement pour le lac Ontario semble balancé parce que la production primaire y avait été incluse comme entrée. En réalité, les pertes calculées de CO_2 s'échappant dans l'atmosphère font que les sorties annuelles dépassent de beaucoup les entrées. L'hypothèse que ces pertes de CO_2 sont un résultat direct de la production primaire n'est pas conforme aux autres données.

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THE task of calculating a carbon budget for Lake Ontario is immense but the results are very important because energy used to support the structure and function of ecosystems is transmitted via carbon fluxes through the food chain. In addition, the net carbon balance of lake ecosystems determines the extent of oxygen depletion and may also influence the return of substances from the sediments.

A recent carbon budget for Lake Ontario reported by Robertson and Eadie (1975) appears to indicate an approximate balance between inputs and outputs. The carbon inputs to the lake used in calculating the budget were inorganic and organic forms in rivers and lake primary production. Carbon outputs considered were inorganic and organic forms in rivers, gaseous CO_2 exchange, $CaCO_3$ precipitation, and sedimentation. While the achievement of a balance appeared to lend some credibility to the various measurements, the inclusion of primary production as an input to these calculations unfortunately produces major error.

Primary production processes (i.e. photosynthesis and growth of algae) move carbon from the dissolved inorganic form (DIC) to a particulate organic form (POC). The flux of carbon is from water to particles. Primary production alone is neither an input nor an output in a lake carbon budget. Thus, in Robertson and Eadie's budget, primary production should be removed from the list of inputs; if this approach is taken, the annual budget does not balance (Table 1). Approximately equal amounts of carbon enter and exit via rivers, but what is striking about Table 1 is that the amount of carbon leaving the lake via gaseous exchange is equivalent to half the total lost via rivers.

Carbon dioxide exchange with the atmosphere is the one major flux which has not been measured but was estimated using calculations of CO_2 partial pressure (pCO_2), windspeed, and a laboratory diffusion coefficient. According to Robertson and Eadie there is a small CO_2 flux into the lake in the summer and a large flux out in the fall, winter, and spring due to equilibration of the supersaturated hypolimnetic water during mixing. It was assumed that supersaturation of the hypolimnion was caused by the decomposition of part of the organic matter formed by primary production. The magnitude of the net gas loss is difficult to explain when primary production is removed from the inputs. Some of the problems are apparent upon examination of hypolimnion O_2 changes.

A condition of hypolimnetic CO_2 supersaturation resulting from decomposition should have been accompanied by a corresponding decrease in oxygen amounts. The average hypolimnion O_2

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TABLE 1. Carbon budget for the average year (kilograms C × 10^{-8}) (from Robertson and Eadie 1975).

Input			Output					
Inorganic	Organic		Inorganic			Organic		
Rivers	Rivers	Primary production	Rivers	Gas	$CaCO_3$	Rivers	Sediment	Net
49.8	6.3	33.4	48.6	27.6	0.4	4.4	1.9	6.6[a]
	89.5			82.9				−28.6[b]
Ratio of Input–Output with primary production is 1.08.								×
Ratio of Input–Output without primary production is 0.68.								

[a]With primary production.
[b]Without primary production.

depletion rate in Lake Ontario for the years 1969–71 was 0.53 mg/ℓ per mo (Hugh Dobson, Process Research Division, CCIW, Burlington, personal communication). Assuming a respiratory quotient of 1, the amounts of carbon oxidized in the hypolimnion, and hypolimnion plus thermocline, were 9.1 and 15.8 g/m^2 per mo, respectively. These rates, over 4 summer mo, multiplied by the area of the lake, 18,800 km^2, indicate the oxidation of 7–12 × 10^8 kg of carbon, which is only 24–44% of the total C lost as CO_2 and equivalent to 37–66% of the summertime primary production. Thus, the amount of CO_2 lost is more than could have been produced by decomposition in the hypolimnion. Epilimnion carbon fluxes seem to confirm that phytoplankton are not involved in the net CO_2 loss.

A net downward flux of phytosynthetically fixed carbon sufficient to cause the subsequent CO_2 outflux would deplete the DIC of the top 10 m by 40% given the small summer CO_2 influx claimed by Robertson and Eadie. The amount of fixed carbon required to cause all of the hypolimnetic O_2 demand would have depleted surface water DIC by 15–26%. There are few direct measurements of DIC in Lake Ontario surface waters, but Weiler (1974) found that the difference between March and July concentrations was only 7% and that September concentrations were higher than those in July (Weiler, Applied Research Division, CCIW, Burlington, personal communication). Also, the scanty data available indicate depletion of a similar proportion of calcium, probably by $CaCO_3$ precipitation. Thus, given the small summertime CO_2 flux, the changes in DIC and calcium are inconsistent with the notion that most or all of the fixed carbon decomposed in the hypolimnion. This means that either CO_2 influx was much higher than claimed, or much of the fixed carbon was metabolically recycled in the epilimnion. Recent experiments (Charlton unpublished data) using bottle enclosures and in situ O_2 changes support the latter alternative. Undoubtedly many of the problems with carbon budgets stem from the difficult CO_2 flux estimates.

Estimates of CO_2 flux depend on the transfer coefficient/wind speed relationship and the estimation of pCO_2. Variation of the transfer coefficient appears to be ±50% and the calculation of pCO_2 is extremely sensitive to errors in pH measurement (Weiler 1975). Thus, the accuracy of flux estimates is limited and more work needs to be done in this field. It is perhaps instructive to view flux estimates in relation to the total carbon pool of lakes.

The yearly CO_2 outflux claimed by Robertson and Eadie is 7% of the total DIC contained in Lake Ontario. Weiler's (1975) estimate is about 4 times greater and, for Lake Erie, is equivalent to the entire DIC pool! Net losses of these amounts of carbon would be readily detectable as a change in DIC but this has not been reported. If the CO_2 fluxes are real, the winter outflux cannot be attributed to primary production processes. Certainly more work must be done to refine CO_2 flux estimates and explain their relative magnitude.

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Thyroid Activity of Alewives (*Alosa pseudoharengus*) and Rainbow Smelts (*Osmerus mordax*) in the Great Lakes

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SONSTEGARD, R., J. F. LEATHERLAND, AND R. MOCCIA. 1977. Thyroid activity of alewives (*Alosa pseudoharengus*) and rainbow smelts (*Osmerus mordax*) in the Great Lakes. J. Fish. Res. Board Can. 34: 1242–1244.

Thyroid glands, collected in 1974 and 1976 from sexually mature prespawning alewives (*Alosa pseudoharengus*) captured in lakes Ontario, Huron, and Michigan and from sexually mature, spawning rainbow smelts (*Osmerus mordax*) from lakes Ontario and Erie, showed no evidence of the thyroid exhaustion described in these species collected from identical sites and seasons in 1952. The observations suggest a change in the apparent thyroid activity of these species from those in earlier studies, and that the annual mortality of alewives is not directly related to an inability to produce sufficient thyroid hormone.

Key words: alewives, rainbow smelts, thyroid, mortality, Great Lakes

SONSTEGARD, R., J. F. LEATHERLAND, AND R. MOCCIA. 1977. Thyroid activity of alewives (*Alosa pseudoharengus*) and rainbow smelts (*Osmerus mordax*) in the Great Lakes. J. Fish. Res. Board Can. 34: 1242–1244.

Les glandes thyroïdes prélevées en 1974 et 1976 de gaspareaux (*Alosa pseudoharengus*) mûrs avant la fraie capturés dans les lacs Ontario, Huron et Michigan, et d'éperlans arc-en-ciel (*Osmerus mordax*) mûrs en voie de fraie dans les lacs Ontario et Erié n'offrent aucune indication de l'épuisement thyroïdien décrit chez ces espèces capturées à des sites et des saisons identiques en 1952. Les observations suggèrent qu'il y eut changement dans l'activité thyroïdienne apparente de ces espèces par rapport à celle observée antérieurement, et que la mortalité annuelle des gaspareaux n'est pas directement liée à une incapacité de produire suffisamment d'hormone thyroïdienne.

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HOAR (1952) described an active state of thyroid in alewives (*Alosa pseudoharengus*) and rainbow smelts (*Osmerus mordax*) collected from the Great Lakes compared with similar specimens collected from the sea. He deduced that this could be a symptom of low iodine levels in the Great Lakes and suggested that this hypothyroid condition, "exhausted thyroid," in alewives may account for the annual mortalities in this species (Hoar 1952, 1973). This note compares the thyroid condition of prespawning alewives and spawning smelts collected from several sites on the Great Lakes, including some made at the same time of year and location as Hoar's (1952) collection.

Materials and Methods

Samples of smelt and alewives were collected from a number of locations on the Great Lakes (see Table 1). The alewife populations studied (prespawning adults) were all suffering high mortalities at the time of collection (many were captured by dipping at the surface as they were weakly spiralling about in the final stages of dying).

The thyroid region was taken from five to eight fish randomly selected (including males and females) from each collection site, and fixed in Bouin's fluid. The tissues were decalcified, embedded in Paraplast, sectioned at 7 μm, and stained with hematoxylin and eosin. Epithelial cell heights and follicle diameters were measured in five randomly selected fish from each 1976 collection site. Twenty measurements were made of epithelial cell height and 10 of follicle diameter in each fish by means of an ocular micrometer. Data of epithelial cell heights and follicular diameter were separately compared by one-way analysis of variance with subsamples (Steel and Torrie 1960).

Results and Discussion

In all the fish examined the thyroid consisted of small numbers of follicles of homogenous colloid surrounded by cuboidal or moderately

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TABLE 1. Thyroid epithelial cell height and follicle diameter in alewives (*Alosa pseudoharengus*) and rainbow smelts (*Osmerus mordax*) from the Great Lakes.

Collection site	Date of collection	Epithelial cell height[a] (μm)	Follicle diam[a] (μm)
Alewives[b] (sexually mature prespawning fish)			
Burlington Bay,[c] Lake Ontario	30.5.74	—	—
Burlington Bay,[c] Lake Ontario	13.5.76	6.3±2.6	133.2±23.7
Owen Sound, Lake Huron	1.6.74	—	—
Goderich, Lake Huron	20.5.76	9.0±2.6	121.9±23.7
Leland, Lake Michigan	12.6.76	9.7±2.6	138.8±23.7
Smelts (sexually mature spawning fish)			
Burlington Bay, Lake Ontario	29.4.76	10.4±2.6	111.9±23.7
Normandale, Lake Erie	4.5.76	9.4±2.6	133.1±23.7

[a]Data expressed as mean ± standard error of mean. Standard error of mean was calculated according to the method recommended by Steel and Torrie (1960) which is appropriate for data compared by analysis of variance with subsamples.

[b]Alewife collections were made from sexually mature adults suffering high mortalities and include moribund specimens from each site.

[c]Samples collected at same site and season as Hoar (1952).

columnar epithelial cells. There was no evidence of hyperplasia or marked vacuolation of the colloid in any of the samples. There were no significant differences in cell height or follicle diameter between any of the groups (Table 1). These data are at variance with those reported by Hoar (1952, 1973) who showed hypertrophy and hyperplasia of thyroid tissue in Lake Ontario alewives (and, to a lesser extent, in Lake Huron smelts), including a virtually total depletion of colloid material in the sexually mature fish from the Great Lakes. Epithelial cell heights in alewives in Hoar's (1952) collection (calculated from figures in that report) were between 11 and 17 μm, which were greater than in any fish or groups of fish examined in this study (see Table 1). Moreover, follicle diameters in smelts and alewives studied by Hoar (1952) were smaller than in the fish used in this study.

The alewife populations studied in these investigations were all suffering high mortalities at the time of collection but none of the moribund fish exhibited hyperplastic, colloid-depleted, thyroid glands. Thus, it does not appear that the "exhausted thyroid" condition described by Hoar (1952, 1973) is a major contributing factor to the alewife mortalities in the Great Lakes.

The usefulness of histological criteria to assess thyroid activity is somewhat questionable (Gorbman 1969). In addition, thyroid activity in teleosts is thought to be affected by the state of sexual maturation, feeding and migration (Gorbman 1969; Narayansingh and Eales 1974a, b; Sonstegard and Leatherland 1976). However, the observations reported here clearly indicate a difference in the thyroid state of the fish collected in 1974 and 1976 compared with the observations made nearly 25 yr ago by Hoar (1952) in fish that had been captured at the same sites and time of year.

The apparent change in the thyroid response of the two species in 1974 and 1976 compared with the 1952 collection may represent a change in the gene pool, although natural selection over a 25-yr period seems unlikely. Conversely, it may suggest that changes of unknown nature have occurred in the lake system which have enabled these species to retain a euthyroid state without reverting to hyperplasia. No interlake or species differences were detected in the histology of the thyroid glands which suggests that goiterogens in

the lakes do not appear to be in concentrations sufficient to elicit a response in these two species.

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Ultraviolet Treatment of Water for Destruction of Five Gram-Negative Bacteria Pathogenic to Fishes

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BULLOCK, G. L., AND H. M. STUCKEY. 1977. Ultraviolet treatment of water for destruction of five gram-negative bacteria pathogenic to fishes. J. Fish. Res. Board Can. 34: 1244–1249.

Filtration (25 nm) and ultraviolet irradiation dosages of 13,100–29,400 microwatt seconds per square centimetre ($\mu W \cdot s \cdot cm^{-2}$) effected a 99.98–100% reduction of five gram-negative fish pathogens — *Aeromonas salmonicida*, *A. hydrophila*, *Vibrio anguillarum*, *Pseudomonas fluorescens*, and the enteric redmouth organism in 12.5°C clear spring water or spring water containing particulate matter. Filtration and a dosage of 4500 $\mu W \cdot s \cdot cm^{-2}$ killed 99.83–100% of test strains in spring water and 4000–4750 $\mu W \cdot s \cdot cm^{-2}$ killed 99.33–99.99% in water with particulate matter. Irradiation of unfiltered water containing particulate matter was less effective, especially at dosages of 5000 $\mu W \cdot s \cdot cm^{-2}$ or less, which killed 97–99.94% of strains. Filtration and 13,100 $\mu W \cdot s \cdot cm^{-2}$ irradiation of water containing *A. salmonicida* prevented transmission of furunculosis.

Key words: ultraviolet irradiation, bacterial fish pathogens, water disinfection

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La filtration (25 nm) et l'irradiation aux rayons ultraviolets à des dosages de 13 100–29 400 microwatts par seconde par centimètre carré ($\mu W \cdot s \cdot cm^{-2}$) causent une réduction de 99.98–100% de cinq bactéries Gram négatif pathogènes des poissons — *Aeromonas salmonicida*, *A. hydrophila*, *Vibrio anguillarum*, *Pseudomonas fluorescens* et l'organisme de la bouche rouge entérique dans de l'eau de source claire à 12.5°C ou dans de l'eau de source contenant de la matière particulaire. La filtration et un dosage de 4 500 $\mu W \cdot s \cdot cm^{-2}$ tuent 99.83–100% des lignées

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d'essais dans de l'eau de source, et 4000–4750 $\mu W \cdot s \cdot cm^{-2}$ tuent 99.33–99.99% dans de l'eau contenant de la matière particulaire. L'irradiation d'eau non filtrée contenant de la matière particulaire est moins efficace, surtout à des dosages de 5000 $\mu W \cdot s \cdot cm^{-2}$ ou moins, qui tuent 97–99.94% des lignées. La filtration et l'irradiation à 13 100 $\mu W \cdot s \cdot cm^{-2}$ de l'eau contenant *A. salmonicida* empêchent la transmission de la furonculose.

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THE use of ultraviolet (UV) irradiation at or near 2537 Å has received attention for destroying fish-pathogenic organisms 15 μm or smaller. Burrows and Combs (1968) recommended UV for hatchery reuse systems to prevent disease. Herald et al. (1971) used UV irradiation to effect a 98% reduction of bacteria in a closed seawater aquarium system.

Treatment of hatchery water with dosages of 35,000 $\mu W \cdot s \cdot cm^{-2}$ controlled *Ceratomyxa shasta* and killed 75% of *Nanophyetes cercariae* (Burrows and Combs 1968). Hoffman (1974), who reviewed the use of UV in fish cultural practices, reported that 35,000 $\mu W \cdot s \cdot cm^{-2}$ prevented transmission of *Myxosoma cerebralis*. Kimura et al. (1976) found that 23,100 $\mu W \cdot s \cdot cm^{-2}$ effected a 99.9% reduction of five gram-negative pathogens. Although relatively high dosages of UV are known to kill fish pathogens effectively and UV irradiation is used at several hatcheries for disinfection of water supplies, the minimum effective exposure level has seldom been determined (Hoffman 1974). We tested the effects of various UV dosages on known numbers of five gram-negative pathogens and the effectiveness of UV in preventing fish-to-fish transmission of *Aeromonas salmonicida*.

Materials and methods — The following gram-negative fish pathogenic bacteria were tested: *A. salmonicida*, *A. hydrophila*, *Pseudomonas fluorescens*, *Vibrio anguillarum*, and the enteric redmouth (ERM) bacterium. Two strains of each organism were used in one series of tests and three strains in another series. Cultures were taken from stocks maintained at −80°C, checked for purity on brain heart infusion agar (BHIA), grown on BHIA for 24 h at 20 or 30°C, suspended in sterile saline, and adjusted to 10% transmittance at 525 nm.

Forty litres of 12.5°C spring water of known composition (Warren 1963) and with a transmittancy of 95% that of deionized water were placed into a 57-ℓ plastic aquarium. The 95% transmittancy is equivalent to 4 Jackson Turbidity Units (JTU) as determined on a colorimeter at 450 nm and a table calibrated from standard formazin solutions (Hach procedures for water and sewage, Hach Chemical Company, Ames, Iowa). Sufficient culture suspension (5–7 ml) was added to provide a count of viable bacteria of 10^4 to $10^5 \cdot ml^{-1}$. The water was then pumped through a 25-nm porosity filter (Micro-Wynd II D-PPPF G. P. Dempler Co., Bridgeville, Pa.) into a model 500 UV purifier, furnished by the Ultradynamic Co., Inc. The UV unit contained one P-247 bulb inside a quartz cylinder. The UV purifier was fitted with a Model GL-100 intensity meter which has a narrow-band spectral response at 2537 Å. The UV dosage for each trial was calculated by multiplying the reading on the intensity meter (in microwatts per square centimetre) by the transit time of the water. In all tests water was pumped at 56.8 $\ell \cdot min^{-1}$. Transit time was 3.2 s. All test strains were exposed to the highest and lowest dosage obtainable with the UV purifier. We turned the purifier on 30 min before each trial to insure full intensity. Bacteria-laden water was then pumped for 20 s and a 200-ml sample taken aseptically. To obtain the lowest dosage, we used a rheostat to reduce voltage to the purifier. The test water was again pumped and a second sample taken after 20 s.

Samples of 200 ml were also taken aseptically from raw spring water and from water containing test bacteria that was filtered but not UV treated. The number of viable bacteria in each sample was determined by making serial tenfold dilutions in 0.5% tryptone broth and then preparing triplicate pour-plates for diluted samples. We used BHIA cooled to 42°C for all organisms except *A. salmonicida*, for which because of its heat lability, we used 12% gelatin, instead of agar, in BHIA broth. Plates prepared from the test samples were incubated at 15°C (*A. salmonicida*), 20°C (*P. fluorescens*), or 30°C (other three organisms). Colonies were counted after 72 h incubation only on plates showing 30–300 colonies. Since small (1.0 ml) samples of irradiated water were taken for determination of viable bacteria by plate count, we also estimated the number of surviving bacteria in the high dosage samples by the most probable number technique of Hoskins (1940), in which 30.5 ml were taken from each irradiated sample.

We repeated the above procedure, using three strains of each organism suspended in spring water taken from a tank containing adult rainbow trout (*Salmo gairdneri*). Trials were carried out with bacteria suspended in 120 ℓ of tank water, held in a stainless steel trough. In contrast to the high transmittance of the spring water, that of the tank water was only 50–60% (85–100 JTU) that of deionized water because of the presence of suspended material (primarily uneaten food and feces). The effectiveness of the high and low UV dosages was determined with and without the 25-nm filtration, and the number of surviving bacteria was determined by pour plate only.

To demonstrate that surviving bacteria were those that had been added, we identified representative colonies, using the scheme of Shotts and Bullock (1975) and specific antisera.

In testing the efficiency of UV irradiation for preventing transmission of furunculosis, 12.5°C water from a tank containing brown trout (*S. trutta*) with furunculosis was passed through the filter and UV unit (13,100 $\mu W \cdot s \cdot cm^{-2}$) and used to fill two drained (57 ℓ) aquaria, each containing 200–225 (908 g) fingerling Atlantic salmon (*S. salar*), 5–7 cm long. Salmon were exposed to the irradiated water for 2 min and spring water was then turned on. Salmon were exposed to irradiated water from the tank with brown trout in this manner 5 times over a period of 9 days. Two tanks of salmon were similarly treated with water that was filtered but not irradiated. Dead salmon were collected daily for up to 4 wk and cultured for *A. salmonicida*.

The presence of viable bacteria in water from the tank containing brown trout infected with furunculosis was determined before and after irradiation by the pour-plate method. The density of *A. salmonicida* in water before irradiation was estimated by counting colonies surrounded by light brown pigment. Since irradiation may have affected pigment production, representative colonies from plates of irradiated water samples were identified to make sure none were *A. salmonicida*.

Results — Filtration and UV irradiation of clear spring water at dosages of 21,000–24,000 $\mu W \cdot s \cdot cm^{-2}$ killed 99.9–100% (values of 99.999% or greater are considered 100%) of all test bacteria, while at a dosage of 4500 $\mu W \cdot s \cdot cm^{-2}$ 99.83–100% of test strains were killed (Fig. 1A). There was agreement between counts obtained by most probable number and plate count procedure, indicating the 1.0-ml samples taken for plate counts were reflective of UV effectiveness. Bacteria surviving irradiation of clear spring water were found to be test organisms and not contaminants.

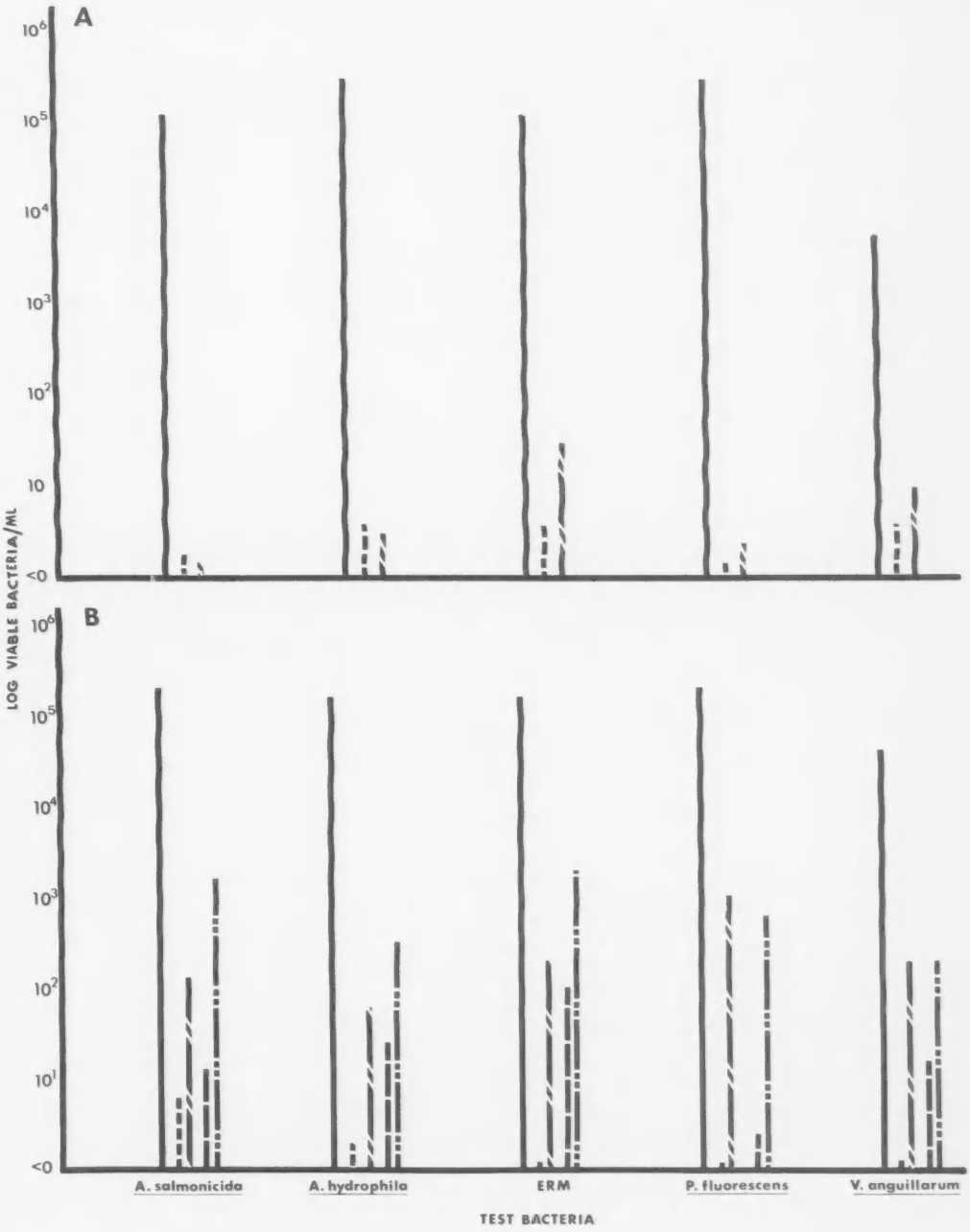
When test strains were added to water containing suspended organic matter, filtration and UV dosages of 13,100–29,400 $\mu W \cdot s \cdot cm^{-2}$ resulted in 99.98–100% destruction, while 4000–4750 $\mu W \cdot s \cdot cm^{-2}$ killed 99.33–99.99% of all strains (Fig. 1B). Without prior filtration, UV treatment of water containing organic matter killed 99.93–100% of bacteria at 11,600–29,700 $\mu W \cdot s \cdot cm^{-2}$ but 99.00–99.94% at 3300–5300 $\mu W \cdot s \cdot cm^{-2}$ (Fig. 1B). The range of UV dosages was greater in water containing particulate matter than in spring water because the amount of particulate matter varied. Also, the counts of raw tank water were much higher than those for spring water (up to $10^5 \cdot ml^{-1}$, in comparison with $<10^2 \cdot ml^{-1}$ and, in contrast to results obtained with spring water, the bacteria surviving irradiation in tank water were rarely the test bacteria.

When used in conjunction with filtration, irradiation at 13,100 $\mu W \cdot s \cdot cm^2$ prevented transmission of furunculosis. Salmon receiving only filtered water sustained a 98.5% mortality (Fig. 2). Total bacterial counts of water from the tank containing diseased brown trout were 4.8×10^4 to $2.9 \times 10^5 \cdot ml^{-1}$, whereas the counts of *A. salmonicida* were estimated at 4×10^3 to $1.2 \times 10^5 \cdot ml^{-1}$. Total bacteria were reduced 99.98%, and since no *A. salmonicida* were detected among bacteria surviving the UV, we assume either a 100% kill of the pathogen or a level of survivors too low for detection by our procedures.

Discussion — Our results showed that with prior filtration a dosage of 13,100 $\mu W \cdot s \cdot cm^{-2}$ killed 99.99–100% of all test strains suspended in water with organic material and that dosages of 21,000–24,000 $\mu W \cdot s \cdot cm^{-2}$ did not consistently kill 100% of strains even in clear spring water. Kimura et al. (1976) also obtained 99.99% kills of bacteria in pond water with a dosage of 13,500 $\mu W \cdot s \cdot cm{-}^2$ but the level of fish pathogens in the water was not known. The 13,100 $\mu W \cdot s \cdot cm^{-2}$ level also prevented transmission of furunculosis to Atlantic salmon. Even though the salmon were exposed intermittently to irradiated water, the machine was used at twice the recommended flow rate and disease transmission was still prevented.

We found that filtration of water with organic matter and UV dosages as low as 4000 $\mu W \cdot s \cdot cm^{-2}$ killed 100% of some *P. fluorescens* and *A. salmonicida* strains, while other test bacteria

FIG. 1. A, Effect of 25-nm filtration and 21,000–24,000 $\mu W \cdot s \cdot cm^{-2}$ (▬▬) or 4500 $\mu W \cdot s \cdot cm^{-2}$ (▰▰) on viable counts of five gram-negative fish pathogens — *Aeromonas salmonicida*, *A. hydrophila*, *Vibrio anguillarum*, *Pseudomonas fluorescens*, and the enteric redmouth organism — in 12.5°C spring water. Solid line represents counts of viable bacteria before irradiation. Counts are averages of triplicate plate counts of two strains of each pathogen. B, Effect of ultraviolet dosages with and without prior 25-nm filtration on viable counts of five gram-negative fish pathogens in 12.5°C water containing suspended organic material: (▬) counts before irradiation; (▬ ▬) after filtration and 13,100–29,400 $\mu W \cdot s \cdot cm^{-2}$; (▰▰) after filtration and 4000–4700 $\mu W \cdot s \cdot cm^{-2}$, (▬ ▬) after 11,600–29,700 $\mu W \cdot s \cdot cm^{-2}$; and (▬ ▬ ▬) after 3300–5300 $\mu W \cdot s \cdot cm^{-2}$. Counts are averages of triplicate plate counts of three strains of each pathogen.


A
B
LOG VIABLE BACTERIA/ML
10^6
10^5
10^4
10^3
10^2
10
<0
10^1
A. salmonicida
A. hydrophila
ERM
P. fluorescens
V. anguillarum
TEST BACTERIA

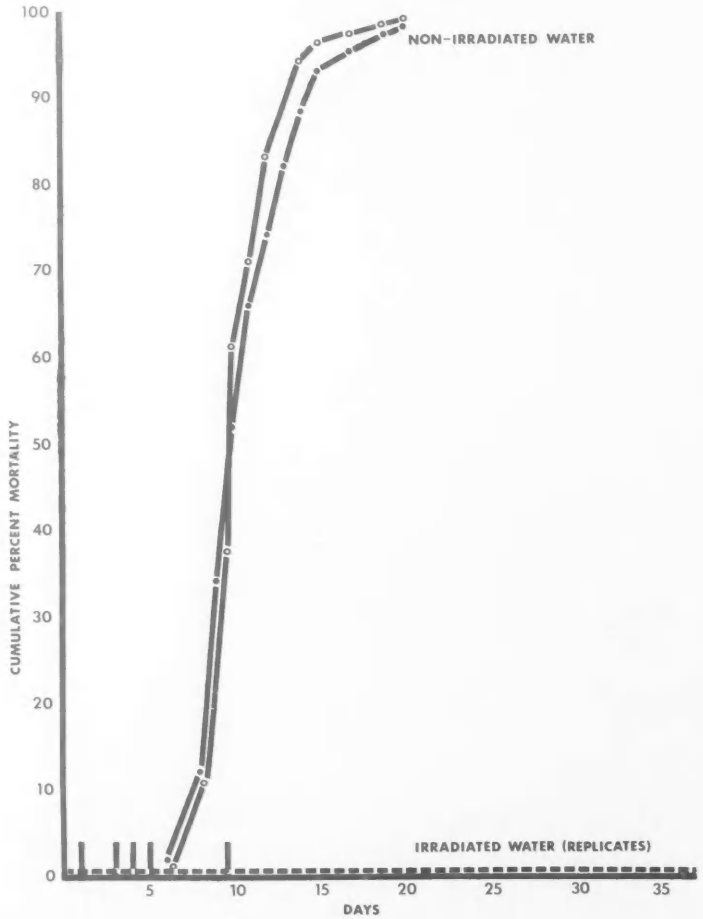


FIG. 2. Efficacy of 25-nm filtration and ultraviolet (13,100 $\mu W \cdot s \cdot cm^{-2}$) treatment of 12.5°C spring water containing *A. salmonicida* in preventing transmission of furunculosis to fingerling Atlantic salmon (*Salmo salar*). Vertical bars at the base show days on which salmon were exposed to irradiated or non-irradiated water.

were reduced by 99.83–99.99%. The significance of these percentage kills are not known at this time since it is difficult to predict the number of bacteria needed to transmit disease. For example, a 99.99% kill of a pathogen at a density of $10^4 \cdot ml^{-1}$ would leave only 10 bacteria$\cdot ml^{-1}$. However, if the pathogen were virulent and with the potential amplification of the surviving bacteria in fish under intensive culture, this density of bacteria may still transmit disease. Since we could not culture *A. salmonicida* after irradiation of tank water containing furunculosis infected trout, we assume that even if the furunculosis bacterium were present in the irradiated water, the level was too low to initiate infection in the salmon within 3 wk after the last exposure.

While UV irradiation of filtered water has been shown effective in killing known numbers of bacterial pathogens and effecting disease control, the present studies were conducted on a small scale. Larger pilot type studies are needed to judge the effectiveness of UV irradiation under practical hatchery conditions. As pointed out by Conrad et al. (1975), who showed the effectiveness of ozone in killing fish pathogens, there are many factors to be evaluated before using ozone

on a large scale. The same is true for UV irradiation, since its effect will have to be determined on the viral fish pathogens and problem parasites such as *Ichthyophthirius*.

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Comments on "Chemical Oceanography in Canada" (C. R. Mann)

In writing on the subject of chemical oceanography I agree that it is probably impossible to satisfy every scientist's concept of the subject, although it may be possible to offer alternative viewpoints. Dr Mann's report on this subject (J. Fish. Res. Board Can., Vol. 33: 1451–1469) emphasizes chemical oceanography as the most recently developed oceanographic discipline in Canada (p. 1452). This is a restriction that implies that in the past a lot of people who thought they were studying the ocean's chemistry, were not. His concept of chemical oceanography is further limited to the "water sphere" (p. 1453). I find it difficult to agree with either the discipline or location restrictions as given in this report.

Dr Mann eliminates from his discussion "those whose interest is confined to the food chain, and others who are primarily concerned with sedimentary geochemistry" (p. 1453). Fortunately, while imposing these restrictions, he does not abide by them since it is possible to find on practically every page, some mention of the food chain and sediments (e.g. p. 1458, "Particular emphasis should be given to . . . the interstitial water of sediments.", or p. 1459, "These processes are important because the organic matter thereby becomes available to filter feeding organisms. . ."). By eliminating the chemistry of the food chain and sediments from this report, Dr Mann fails to bring out a point recognized much earlier by Sverdrup et al. (1942), that the oceans are a unified system in which the chemistry cannot be separated from the hydrosphere, biosphere, and geosphere. Thus, chemistry is the most interdisciplinary of the oceanographic sciences and its discussion should not be limited by artificial boundaries imposed around sediments or the biota. This elimination of subject matter in Dr Mann's report has also resulted in the elimination of certain scientists and programs that should be considered part of the chemical oceanographic community in any country (e.g. Dr V. Zitko's work on marine pollution at the St. Andrew's Biological Station is not included under the work of institutions described on p. 1464 and 1465; neither is there any mention of private enterprise research by such companies as Seakem, whose only business is the chemical analysis of sea water). Also, surprisingly absent from the report is any mention of photochemical reactions at the sea surface and the industrial use of sea water as a source of certain important chemicals.

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On the question of a distinct chemical oceanographic discipline, my difficulty in understanding who should be included in such a discipline starts with Dr Mann's use of the term "biochemist," for example on p. 1463, ". . . there are biochemists associated with fisheries who undertake some studies of the ocean's chemistry as part of their main interest in the food chain." Although biochemistry may appear as a convenient contraction of biological chemistry (and is in fact referred to as such in the dictionary), it is really an inappropriate use of what has become a well-defined discipline. Biochemistry, as taught in university departments of biochemistry, deals with *within* organism chemical reactions concerning such subjects as enzyme kinetics, protein chemistry, steroid chemistry, and so on. Thus reference to biochemists studying the "ocean's chemistry," or the "food chain," is misleading because the first is an environment and the second is largely a *between* organism relationship. The study of food chains is a behavioral, physiological, and nutritional problem, often involving analytical chemistry in the same way as agricultural chemists apply chemistry to biological problems (but they do not call it biochemistry simply because it is biologically applied chemistry). There are in fact very few biochemical studies on subjects that could be related to the food chain. On the other hand, there is a large number of scientists in biology who are using chemical methods in their work. In the Abstract, Introduction, and on p. 1467, Dr Mann emphasizes that "the most significant advance has been the recognition of chemical oceanography in several of the oceanographic institutes as a discipline in oceanography to be pursued its own right." The more obvious recognition is, however, left unstated, viz. that most chemical oceanography has been done in the past as part of other oceanographic programs (particularly geological and biological) and that this situation is in fact unlikely to change in the foreseeable future. In fact, as a highly interdisciplinary and applied science it would be undesirable to see chemical oceanography develop as an elitist profession, limited in its role either by its area of interest or by the institutionalization of its members.

Sverdrup, H. V., M. W. Johnson, and R. H. Fleming. 1942. The oceans — their physics, chemistry and general biology. Prentice Hall Inc., Englewood Cliffs, N.J. 1087 p.

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Dr Mann's review of chemical oceanography in Canada is a commendable document on a discipline that does not have well-defined boundaries with other aspects of oceanography. This letter is written to supplement his review with our current thinking and recent developments in the Pacific Region. I concur with his views that chemical oceanography is understrength in general in Canada. In particular, the Pacific Region, with a force of only a quarter of the nation's chemical oceanographers, has to cover an oceanic regime comprising the northeast Pacific Ocean, the western arctic waters, and B.C. coastal waters comparable to the Atlantic seaboard.

Marine chemistry on the west coast has a strong interdisciplinary tradition, dated back to pioneer work by the late J. D. H. Strickland on seawater analysis and the concept of marine food chain. To us, marine chemistry is part of an integrated study of the ocean in the service of man. Understanding the oceanic distribution and processes is our goal. Marine chemistry (or geochemistry, chemical oceanography, biological chemistry) is nothing more than a tool that happens to be useful to our desire to harness the ocean for beneficial uses. It is exceedingly difficult to understand chemical processes in the ocean water without becoming deeply involved in the sedimentary geochemical processes and the biochemical processes going on at the same time. Sea water is a thick soup that is the outcome of geological processes of millions of years, geochemical reactions of thousands of years, chemical changes of great variability and modification by the influence of plants and animals in a wide range of time scales. Chemical studies of the ocean lose effectiveness and perspective if restricted to the water sphere alone.

On the west coast, chemical oceanography in government laboratories has been pursued with parallel development in the strength of private consulting firms. The science requires a calibre to measure its effectiveness more than just counting the number of Ph.D. workers, especially inexperienced pure chemists. It requires veteran chemical oceanographers at the helm, who understand the limitations of chemistry and shipboard operations in the face of complex processes in a vast volume of the ocean — often a chemical oceanographer by training or a chemist who has picked up seagoing experience in numerous extended cruises. It also needs chemical oceanographers who organize and execute difficult sampling, shipboard and laboratory analysis, often uninspiring repetitions that form the single, most important basis of our chemical knowledge in the ocean. The success depends not only on thinkers but on dirty field workers as well as good, precise chemists, often at the M.Sc. levels or Institute of Technology chemists with sufficient seagoing experience. Ph.D. degrees, usually required in academic research, are not prerequisites for excellent chemical oceanography. There are research needs on long-term problems as well as short-term environmental studies, both perhaps of the same importance. I.O.U.B.C. (The Institute of Oceanography at University of British Columbia), despite a long-overdue need for expansion in chemical oceanographic studies and staff size, has satisfied our need on the west coast by producing recently three M.Sc. and one Ph.D. workers in chemical oceanographic studies involving trace metals and hydrocarbons. In our opinion, I.O.U.B.C. has been an active force. Perhaps in a low-key, yet very responsible, way they have produced a smaller number of graduates to satisfy the requirement on the west coast which is relatively small due to lack of man years or resources. They should continue to play their successful and responsible role as a center of education and research in marine chemistry in the Pacific Region.

As mentioned in Dr Mann's report, the Ocean Chemistry Division of the Institute of Ocean Sciences, is the major chemical oceanographic group on the west coast. It is exceedingly small in size relative to problem areas, and we appreciate his comments that our chemical group should be much stronger than it now is to meet our regional need in the Pacific, the Arctic, and the B.C. coastal waters. However, we are fortunate in not having to work in isolation because of our proximity to I.O.U.B.C. and U.S. centers such as the University of Washington, N.O.A.A. Fisheries and Marine Centre in Seattle and our association with the C.E.P.E.X. (Controlled Ecosystem Pollution Experiment), an international program sponsored by the U.S. National Science Foundation and managed by I.O.U.B.C. at the site of our Institute. Our C.E.P.E.X. chemical studies of transfer of CO_2, trace metals, and hydrocarbons, have involved international scientists from West Germany, Japan, the U.S., and other parts of Canada. In addition, our small group of ocean chemists has not experienced lack of direction in the need to sort out aspects of research in chemical oceanography that should be pursued. This is perhaps the experience of development in the east coast, but is not necessarily applicable to the west coast because of a fairly early start by the late J. D. H. Strickland and because of a sustained small effort which maintained continuity, at the Pacific Oceanographic Group in Nanaimo and at I.O.U.B.C. The formation of Ocean Chemistry Division in 1970 was not a quantum jump: it has a historical link to our interdisciplinary approach on the west coast through the weathership time-series program. Of course, with new tasks to establish the state of the marine environment, we have developed lines of research on ultra-trace levels of petroleum hydrocarbons and trace metals in the marine environment building our shore contaminant-free laboratories in as early as 1972, now adopted by NRC's Atlantic Regional Laboratory for the Atlantic region, and taking our shipboard clean laboratories in 1975 to Beaufort Sea for baseline hydrocarbon work and in B.C. coastal waters for trace metals in connection with ocean dumping studies. We were probably the first in the world to apply shipboard portable clean laboratories, now being adopted by Kiel University, West Germany, and the Santa Cruz Laboratory of the University of California, USA. Using a unified

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approach in ultra-trace studies to achieve meaningful data, we have established much lower levels of trace metals and hydrocarbons in sea water than previously believed. We are also studying the fluxes of lead, cadmium, and mercury in the marine environment using the C.E.P.E.X. approach and the lead-210 dating technique. These ultra-trace levels are well below levels with known toxic effects on marine biota.

Our current thinking is that it is more important to establish the true levels of pollutants, especially ultra-trace contaminants, through very careful work, and to understand their variability, behavior, and residence time in different oceanic reservoirs, than to start a monitoring program, which implies repetitive analysis of the same ultra-trace parameter by the same chemical technique over a long period of time. Such monitoring appears to be unnecessary in the majority of the marine environments except in water bodies close to severe pollutant sources. A sustained, long-term effort in this type of environmental work acts as an essential insurance policy to ensure a proper care of the health of the ocean and as a capable force in action to investigate when sudden environmental flares occur. Chemical studies of the ocean, we believe, should be part of an integrated approach involving also physical oceanography, marine ecology, and geology in tackling environmental or fisheries problems and will rapidly lose their usefulness and effectiveness if working in isolation from other disciplines.

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BOOK REVIEWS/COMPTES RENDUS

Water Resources of the World. Selected Statistics. *Frits van der Leeden. Water Information Center, Inc., Port Washington, N.Y., 1975. xi + 568 p. $32.50.*

This book includes uniform data, where available, on stream flow, runoff, water demand and water use for public supply, irrigation, industry, and power generation. It also includes a wide array of miscellaneous data. While the book is not meant to be the final answer on all subjects requiring reference to original data, it does, like an encyclopedia, indicate whether the required data exist, and tells where they can be obtained. It does provide answers to almost any other question about water.

The data are clearly identified as to source and date of publication. Although some of the publication dates are 10 or more years old, no attempt is made to imply that the material is more recent. Since the source of the material is indicated in all cases, up-to-date information can be requested if required. However, there may be some problems with translations, as the author has had recourse to some very obscure publications.

I might quarrel with the format in which the data are presented. Almost the entire content of the book is tabular. While this does organize the material effectively, it makes a weary job of finding a particular set of information. The organization of the material on a geographical basis was apparently recognized by the author as being inconvenient for some uses, to the extent that he has organized much of the data by subject at the end of the book.

Other criticisms are that the oceans receive only the briefest mention, and the quality and variety of the data presented vary widely with the area covered. This last, of course, reflects the availability of data, rather than any lack of diligence on the part of the author.

This book is a valuable reference for anyone who deals with water as a resource. Though there is material in it of value to aquatic biologists, I doubt that there is enough to warrant inclusion in a private library, though institutional libraries might well be expected to have the book on hand.

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(R93)

Encyclopaedic Dictionary of Mathematics for Engineers and Applied Scientists. *Edited by I. N. Sneddon. Pergamon Press Ltd., Oxford, 1976. viii + 800 p. $100.*

Scientists and engineers make frequent use of mathematical tools. For many the technique most needed will be only imperfectly remembered; it is for such persons that this book is intended. A large number of entries cover a wide range of topics with an emphasis on those concepts most widely and frequently used in engineering problems. In addition, there is a fairly extensive inclusion of entries covering physical laws as well as a number of borderline topics covering electronic calculators and computing machines.

A serious difficulty, perhaps unavoidable in a dictionary of this sort, is that a multitude of authors have contributed, each with his own style. The result is a rather uneven sequence of entries, some fairly extensive, while others are quite terse and hard to read. To some extent this is intentional. The calculus of variations, for example, can scarcely be covered in a couple of paragraphs. On the other hand, it is questionable whether the two pages or so that are given will be that helpful either. They may provide the reader with some of the main concepts but they are unlikely to be sufficient to help him solve practical problems. The larger topics do include a bibliography, which often tends to be dated. For example, the most recent reference on the calculus of variations is 1956, and this is typical of many of the survey articles.

Editing a work of this type must be an arduous task but the curious reader must wonder how recently some of the entries were written. Some quite topical mathematical techniques, such as similarity methods for solving differential equations, seem to have been missed. The most readable and useful articles this reviewer has read relate to numerical techniques.

Inclusion of numerous articles on fluid dynamics will certainly be a welcome addition for those who work in the aquatic sciences. But there are also some surprising omissions. Particularly disappointing is the neglect of topics related to time series analysis, digital filters, spectral analysis, and so forth. These techniques are widely used and dictionary definitions of frequently used terms would be helpful.

Since the price tag on this book puts it well beyond

the reach of the individual's bookshelf, it is fair to ask whether it is really a worthwhile addition to a library that already has a good handbook of applied mathematics that includes a detailed discussion of methods and techniques. The difference lies partly in the organization of the book and in the range of topics included. The Editor's hope that "an engineer who uses mathematics at any level will find that virtually all his requirements are met in this single volume" seems extravagant. The practical user of mathematical techniques will generally prefer a more coherent approach and grouping of topics together with worked examples. Use of a dictionary increases the likelihood that in looking up a partially remembered technique for solving a problem, a more suitable technique will be missed. This book has a rather extensive cross-referenced index which, if used properly, would offset some of the disadvantages of an alphabetical listing.

On the other hand, the user who seeks rather to learn what is meant by a term will find the dictionary a more accessible source of information, since each entry is self-contained. In this more limited sense the book can serve a useful purpose and may be recommended to libraries, provided that its purchase is not in lieu of more comprehensive texts on applied mathematics.

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(R129)

Zooplankton Fixation and Preservation. *Edited by H. F. Steedman. The UNESCO Press, Paris, 1976. 350 p.*

This volume in the series of monographs on ocean methodology consists of sections by various authors covering nearly all aspects of plankton work, from the initial collection, through many methods of fixation and preservation to mounting and biomass determination. Although much of the material is aimed at the professional, much is also of interest to the amateur. The section on shipboard and curating techniques should be required reading for all technicians who will be collecting plankton, or other organisms.

On reading through the whole work, I found considerable redundancy, with the same recommendations being repeated in different contexts. I lost track of the number of times that 2% to 4% formaldehyde buffered with hexamine or borax was recommended for this taxon or that application. However, since the book is obviously meant to be used as a cookbook, with the user turning directly to the section which interests him, this redundancy is essential.

There were a few minor inadequacies in the book. I would like to see a summary of all the recipes for fixatives, preservatives, stains, embedding media, etc., together with their applications as an appendix. This would make the book easier to use. There were a few cases of authors' taking the shortcut of giving a reference to a technique or recipe, rather than writing the material out in full. There was a degree of unevenness in the detail in which different subjects were covered.

However, in view of the overall excellence of the work, and the magnitude of the subject undertaken, I would recommend this book not only to workers in the field of plankton, but to anyone who is likely to want to preserve any biological material for any purpose.

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(R146)

An Illustrated Key to Freshwater and Soil Amoebae. *F. C. Page. Freshwater Biological Association, Scientific Publication No. 34, The Ferry House, Ambleside, Cumbria, G. B., 1976. 155 p. £2.50.*

This key covers the subclass Gymnamoebia, a group approximately equivalent to the old order Amoebida. Although the taxonomy of the group has not yet stabilized, and in spite of the fact that many amoebae have not been satisfactorily described, this book makes a commendable attempt to bring order to the prevailing confusion.

The method followed is to present different keys to families, to the genera in a family, and to the species in a genus. This, of course, allows at least partial identification of any given specimen. In each part of each key an abundance of descriptive and illustrative material is provided, which allows one to determine if the specimen in hand is indeed the species it keys out to. This is a great comfort to the amateur.

The author goes to considerable trouble to assist the amateur in other ways as well. He makes every effort to avoid the vagueness so common in most keys, where it is assumed that the reader is familiar enough with the material to know, for instance, the difference between a broad and a slender body shape. In the instance cited, the author states that a broad amoeba is one that does not attain a length to breadth ratio of 4, while a slender amoeba exceeds this ratio.

There were some faults in the work. While the author defines many of his terms, he does not define all the terms likely to be unfamiliar to the non-specialist, and the definitions are given in the section titled "Using the Key," rather than in a glossary. He

is not always successful in avoiding vagueness, though in some instances this is obviously due to the inadequacy of the descriptions he had to work with, rather than to any lack of ability or care on his part.

In general, then, this is a carefully constructed, well-written book, and is essential to anyone dealing with soil or freshwater amoebae. However, it is likely to have a rather restricted use, since the key can be used only with live material. This leaves most researchers working with routine limnological samples, at least, without any way to identify amoebae. However, this problem is due to the characteristics of the organisms, rather than to the whim of the author, who would, I am sure, put together a key for preserved amoebae if such a thing were possible.

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(R149)

Books Received/Livres reçus

February 1977

An Illustrated Key to Freshwater and Soil Amoebae. *F. C. Page. Freshwater Biological Association, Ambleside, Cumbria, 1976. 155 p. £2.50.* (A useful guide to the living organisms.)

Marine Recreational Fisheries. *Edited by Henry Clepper. Sport Fishing Institute, Washington, D.C., 1976. vi + 174 p.*

Progress in Oceanography. *Edited by Mary Swallow. Pergamon Press Ltd., Oxford OX3 OBW, 1976. Vol. 7(2). p. 59–90. $6.50.*

The Dermatology of Teleost Fishes: a bibliography. *J. P. Hatton, R. J. Roberts, and A. M. Bullock. University of Stirling, Stirling, Scotland, 1976. 264 p. £4.25.*

Thermal Ecology II. *Edited by Gerald W. Esch and and Robert W. McFarlane. U.S. Technical Information Center, Energy Research and Development Administration, Oak Ridge, Tenn. 37830, 1976. ix + 404 p. $11, foreign $13.50.* (The proceedings of the second thermal ecology symposium contain 57 papers dealing with the environmental impact of electric-power facilities, both nuclear and fossil-fueled; thermal ecology at individual, population, and ecosystem levels; and research reports on specific plants, fish, and shellfish.)

Underwater California. *Wheeler J. North. University of California Press, Berkeley, Los Angeles, London, 1976. 276 p. $5.95.* (A pocketbook guide for scuba divers written in the manner of guides for bird-watchers.)

Zooplankton Fixation and Preservation. *Edited by H. F. Steedman, UNESCO Press, Paris, Paris 75700, 1976. 350 p.* (A comprehensive handbook on all phases of the subject.)

March 1977

The Polychaete Worms. Definitions and keys to the orders, families and genera. *Kristian Fauchald. Natural History Museum of Los Angeles County, Science Series 28: 1–190 + ix. 1977. $6.00.* (Comprehensive coverage of polychaete systematics to the genus level; notes on methods.)

Arctic Land Use Issues. *Edited by Norman E. Pressman. Periodical of the Faculty of Environmental Studies, University of Waterloo, Waterloo, Ontario, N2L 3G1. 1976. Vol. 8(4): 1–181. $9.00/year.* (Papers on arctic conservation areas and man's impact on them.)

Retinas of Fishes. An Atlas. *M. A. Ali and M. Anctil. Springer-Verlag, New York, N.Y. 1976. xiii + 284 p. $49.20.* (A beautifully prepared photographic atlas of the histology of retinas of fishes, including Agnatha and the coelacanth. Information is also given on the relationship of retinal structure to habitat.)

The Ecology of the Seas. *Edited by D. H. Cushing and J. J. Walsh. W. B. Saunders Co., Toronto. 1976. x + 467 p. $19.60.* (Many authors have contributed chapters to this book. Not all facts and concepts are covered, but the present state of quantitative marine ecology is described.)

Assessment of the Arctic Marine Environment. *Edited by D. W. Hood and D. C. Burrell. Occasional Publication #4, Institute of Marine Science, University of Alaska, Fairbanks, Alaska. 1976. xi + 468 p. $25.00.* (This book is based on selected topics from a symposium held August 11–15, 1975 in Fairbanks, in connection with the Third International Conference on Port and Ocean Engineering under Arctic Conditions.)

The Biogeography and Numerical Taxonomy of the Oegopsid Squid Family Ommastrephidae in the Pacific Ocean. *John H. Wormuth. Bull. Scripps Institution of Oceanography Vol. 23. University of California, San Diego. La Jolla, Calif. 1976. 90 p. $3.50.*

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 30, NO. 9 — paper by R. H. Green: *Growth and mortality in an arctic intertidal population of Macoma balthica (Pelecypoda, Tellinidae).*

Page 1347: Table 1, headnote should read "Estimates of growth and maximum age for intertidal *Macoma balthica*. The Churchill values are from the fitted growth curves (see text), and the other values are estimated from the results presented by the cited authors."

VOLUME 32, NO. 12 — paper by J. C. Davis: *Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review.*

Page 2297: Right column, par. 4, line 1, "At 19 C fresh water contains" should read "At 10 C fresh water contains."

VOLUME 33, NO. 6 — paper by J. A. Servizi, R. W. Gordon, I. H. Rogers, and H. W. Mahood: *Chemical characteristics and acute toxicity of foam on two aerated lagoons.*

Page 1288: Left column, par. 2, line 8, "mortality was unexpected" should read "mortality was expected." Correction has been made in the reprint of this paper.

VOLUME 33, NO. 7 — paper by J. G. Stockner and K. R. S. Shortreed: *Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia.*

Page 1557: par. 2, line 6, "0.21 $\mu g \cdot cm^{-2}$" should read "0.09 $\mu g \cdot cm^{-2}$."

VOLUME 33, NO. 7 — note by F. M. El-Shamy: *Analyses of gastric emptying in bluegill (Lepomis macrochirus).*

Page 1630: Résumé, the correct French name for bluegill is "crapet arlequin."

VOLUME 33, NO. 9 — paper by J. H. Vandermeulen and D. C. Gordon Jr.: *Reentry of 5-year-old stranded Bunker C fuel oil from a low-energy beach into the water, sediments, and biota of Chedabucto Bay, Nova Scotia.*

Page 2008: Table 1, boxhead, column 5, "Sediment (*mg/mg*)" should read "Sediment (μg/mg)."

VOLUME 34, NO. 5 — paper by J. W. Cornick and J. E. Stewart: *Survival of American lobsters (Homarus americanus) stored in a recirculating, refrigerated seawater system.*

Page 691: Right column, par. 2, line 5, "In addition, low *pH values increase the ratio*" should read "In addition, high pH values increase the ratio."

VOLUME 34, NO. 7 — paper by D. A. McCaughran and G. C. Powell: *Growth model for Alaska king crab (Paralithodes camtschatica).*

Page 991: Right column, par. 3, line 11,

"$\left\{\frac{1L_i - 70|^{1.7}}{1300}\right\}$" should read "$\left\{\frac{|L_i - 70|^{1.7}}{1300}\right\}$."

Page 993: Left column, par. 2, in-text table, line 1, "$P(M|M,M,L_1)$," should read "$P(M|M, M, L_i)$,".

Page 994: Table 6, line 3, "82.00–33.69" should read "33.69–82.00."

Page 995: Figure 5 caption, "Simulated mean carapace length as a function of age for Kodiak male king crabs" should read "Simulated mean carapace length as a function of age for Kodiak king crabs."

BULLETIN 193 — by Ole A. Sæther: *Nearctic and Palaearctic Heterotrissocladius (Diptera: Chironomidae)*

Page 7: Fig. 9 throughout should read Fig. 8, and Fig. 12 should read Fig. 13.

Page 10: In couplet 7, line 2, Fig. 13F should read Fig. 14F; couplet 8, line 3, (Fig. 11N) should read (Fig. 10N).

Page 30: Under *Cephalothorax*, line 1, (Fig. 10A) should read (Fig. 9A).

Page 32: Line 3, Fig. 10F should read Fig. 9F; under *Head*, line 1, 7, and 8, Fig. 11G, 11M, and 11A should read Fig. 10G, 10M, and 10A, respectively.

Page 37: Under *Genitalia*, line 1, (Fig. 9D, E) should read (Fig. 8D, E); under *Cephalothorax*, line 1, (Fig. 10B) should read (Fig. 9B); under *Abdomen*, line 5, Fig. 10G should read Fig. 9G.

Page 38: Under *Head*, line 1, 6, and 7, Fig. 11H, 11M, and 11B should read Fig. 10H, 10M, and 10B, respectively.

Page 40: Under *Genitalia*, line 1, (Fig. 9A–C) should read (Fig. 8A–C); under *Cephalothorax*, line 1, (Fig. 10C) should read (Fig. 9C); under *Abdomen*, line 6, Fig. 10H should read Fig. 9H.

Page 41: First par., line 1, 5, and 6, Fig. 11I, 11N, and 11C should read 10I, 10N, and 10C, respectively.

Page 46: Under *Head*, line 1 and 7, Fig. 11L and 11F should read Fig. 10L and 10F.

BULLETIN 195 — by Ole A. Sæther: *Revision of Hydrobaenus, Trissocladius, Zalutschia, Paratrissocladius, and some related genera (Diptera: Chironomidae)*

Page 41: First par., line 12 and 13, should read "0–4 below setae of B," not 0–4 below setae of B_1,".

Page 48: First par., line 13, "3 or 4 below setae of B, about 8–10 at apex of B," not "3 or 4 below setae of R_1, about 8–10 at apex of R,".

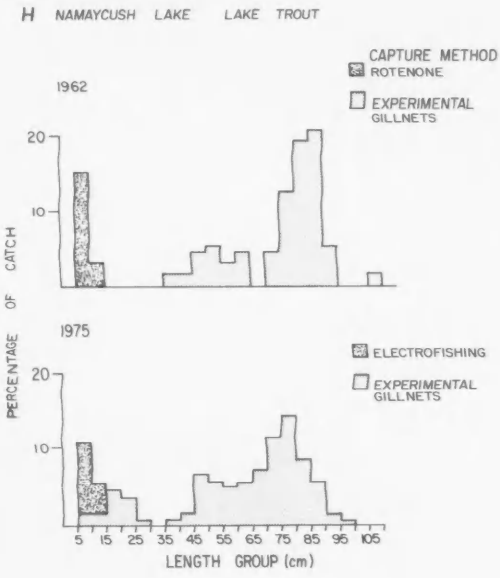
Page 192: Line 1, should read "TA much longer than PP or shorter than PP": key 4, line 1, should read "TA longer than PP, anterior eyespot reniform"; key 4, line 3, should read "TA about $\frac{3}{4}$ as long as PP, anterior eyespot elongated,".

Page 250: Under *Diagnosis*, line 7 and 8, "Sensilla campaniformes about 8 at base of B, about 2 below setae of B, about 7 at apex of B," not "...about 8 at base of B_1, about 2 below setae of B_1, about 7 at apex of B_1."

Page 253: Under *Diagnosis*, line 14, should read "Sensilla campaniformes about 9–12 at base of B," not "Sensilla campaniformes about 9–12 at base of B_1."

VOLUME 33, NO. 11 — paper by L. Johnson: *Ecology of arctic populations of lake trout, Salvelinus namaycush, lake whitefish, Coregonus clupeaformis, Arctic char, S. alpinus, and associated species in unexploited lakes of the Canadian Northwest Territories.*

Page 2470: Figure 7H was omitted.



COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Identification of golden shiner, *Notemigonus crysoleucas*, spotfin shiner, *Notropis spilopterus*, and fathead minnow, *Pimephales promelas* larvae **D. E. Snyder, M. B. M. Snyder, and S. C. Douglas**

The importance of allochthonous particulate carbon pathways in a subalpine lake **R. C. Wissmar, J. E. Richey, and D. E. Spyridakis**

Survival of infectious hematopoietic virus held under various environmental conditions **J. P. Pietsch, D. F. Amend, and C. M. Miller**

Significance of hypochlorous acid in free residual chlorine to the avoidance response of spotted bass (*Micropterus punctulatus*) and rosyface shiner (*Notropis rubellus*) **D. S. Cherry, S. R. Larrick, K. L. Dickson, R. C. Hoehn, and J. Cairns Jr.**

Influence of water temperature on the growth rate of the landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality **G. J. Farmer, F. W. H. Beamish, and P. F. Lett**

Simulation of dispersal of sockeye salmon (*Oncorhynchus nerka*) underyearlings in Babine Lake **S. E. Simms and P. A. Larkin**

Reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia **B. C. Jones and G. H. Geen**

Nearctic and Palaearctic *Paracladopelma* Harnisch and *Saetheria* n.gen. (Diptera: Chironomidae) **J. A. Jackson**

Evidence of a genetic basis for absence of the pelvic skeleton in brook stickleback, *Culea inconstans*, and notes on the geographical distribution and origin of the loss **J. S. Nelson**

Age determination of lingcod (*Ophiodon elongatus*) using dorsal fin rays and scales **R. J. Beamish and D. Chilton**

Suppression of the primary immune response in rainbow trout, *Salmo gairdneri*, sublethally exposed to tritiated water during embryogenesis **J. A. Strand, M. P. Fujihara, R. D. Burdett, and T. M. Poston**

Sealed jar bioassays for pulpmill effluent toxicity: effects of fish species and temperature **M. H. Gordon and D. J. McLeay**

Notes

Ocean migration rates of American shad (*Alosa sapidissima*) **W. C. Leggett**

Simultaneous activity recording of multiple isolated marine organisms in an artificial saltwater recirculating system **S. Rebach**

Reproduction of planted lake trout, *Salvelinus namaycush*, in Gamitagama, a small Precambrian lake in Ontario **C. H. Olver and C. A. Lewis**

Observations on three species of baleen whales off northern Newfoundland and adjacent waters **J. Perkins and H. Whitehead**

Treatments before frozen storage affecting thaw drip formation in Pacific salmon **E. Bilinski, R. E. E. Jonas, Y. C. Lau, and G. Gibbard**

ANNOUNCEMENTS/AVIS

CALL FOR PAPERS
Symposium on the Oceanography of the St. Lawrence Estuary

Papers are solicited for the coming "Symposium on the Oceanography of the St. Lawrence Estuary" to be held April 12–14, 1978, at the University of Quebec at Rimouski, Rimouski, Quebec. Deadline for receipt of abstracts is November 1, 1977. The topics will include all aspects of oceanography: physics, biology, chemistry, pollution, geology, geochemistry, and fisheries research.

Those who are interested in the Symposium or wish to receive further information on the final program should contact the coordinator:

APPEL DE COMMUNICATIONS
Symposium sur l'Océanographie de l'estuaire du St-Laurent

Des papiers sont solicités pour le «Symposium sur l'Océanographie de l'estuaire du St-Laurent» qui se tiendra les 12–14 avril, 1978 à l'Université du Québec à Rimouski, Rimouski, Québec. Les résumés définitifs devront être reçus au plus tard le 1er novembre 1977. Le but de ce Symposium est de faire le point des connaissances actuelles de tous les aspects océanographiques de l'Estuaire, soit l'océanographie physique, biologique, géologique, géochimique, la pollution et les pêches. Ceux qui sont intéressés par le Symposium ou qui veulent avoir d'autres informations sur le programme final devront contacter le coordonnateur:

M. I. El-Sabh
Section d'Océanographie
Université du Québec à Rimouski
Rimouski
Québec G5L 2A1

Planning the Future of the International Decade of Ocean Exploration

The United States program for the International Decade of Ocean Exploration (IDOE) will end as scheduled in 1980. Plans are now underway to design the ocean research program that will follow the IDOE. The goal will be to identify promising directions for marine research, their potential contributions to national ocean interests over the next 5–10 years, and the management approach most appropriate for carrying out these programs.

The basis for this planning effort will be four workshops in each of the major oceanographic disciplines: physical, biological, chemical, and geological. A final workshop, planned and organized by the National Academy of Sciences, will bring together the recommendations from these workshops and report them to the National Science Foundation in late 1977.

The Office for the IDOE invites the interest and participation of the scientific community in planning for the post-1980 program. Comments, recommendations, and requests for additional details may be sent to:

Head, Office for the International
Decade of Ocean Exploration
National Science Foundation
Washington, D.C. 20550, USA

These comments and suggestions will be available as part of the background for these planning activities.

Au-delà de la Décennie internationale de l'exploration des océans

Le programme des Etats-Unis pour la Décennie internationale de l'exploration des océans (DIEO) se terminera, tel que prévu, en 1980. On est présentement à planifier le programme de recherche océanique qui suivra la DIEO. On a comme objectif d'identifier les avenues prometteuses de recherche en sciences de la mer, leurs contributions aux intérêts nationaux vis-à-vis des océans au cours des 5–10 prochaines années, et l'approche de gestion la plus appropriée à l'exécution de ces programmes.

Comme base à cette planification, il y aura quatre ateliers de travail dans chacune des principales disciplines océanographiques : physique, biologique, chimique et géologique. Un dernier atelier de travail, organisé par la National Academy of Sciences, fera la synthèse des recommandations des ateliers de travail et les transmettra à la National Science Foundation à la fin de 1977.

Le Bureau de la DIEO compte sur l'intérêt et la participation de la communauté scientifique dans la planification du programme de l'après-1980. On pourra adresser ses commentaires, recommandations et demandes de détails supplémentaires à:

Head, Office for the International
Decade of Ocean Exploration
National Science Foundation
Washington, D.C. 20550, USA

Les commentaires et suggestions que nous recevrons serviront de toile de fond à cette planification.

Fisheries Research Board of Canada Report Series
Rapports de l'Office des Recherches sur les Pêcheries du Canada

Report No. 1. "The Way Ahead" Symposium on the 75th Anniversary of the Fisheries Research Board of Canada.
(1974, p. 1269–1322, cat. no. Fs 97-10/1, Free)

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